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The spatial patterning of *Hieracium pilosella* invaded short tussock grasslands

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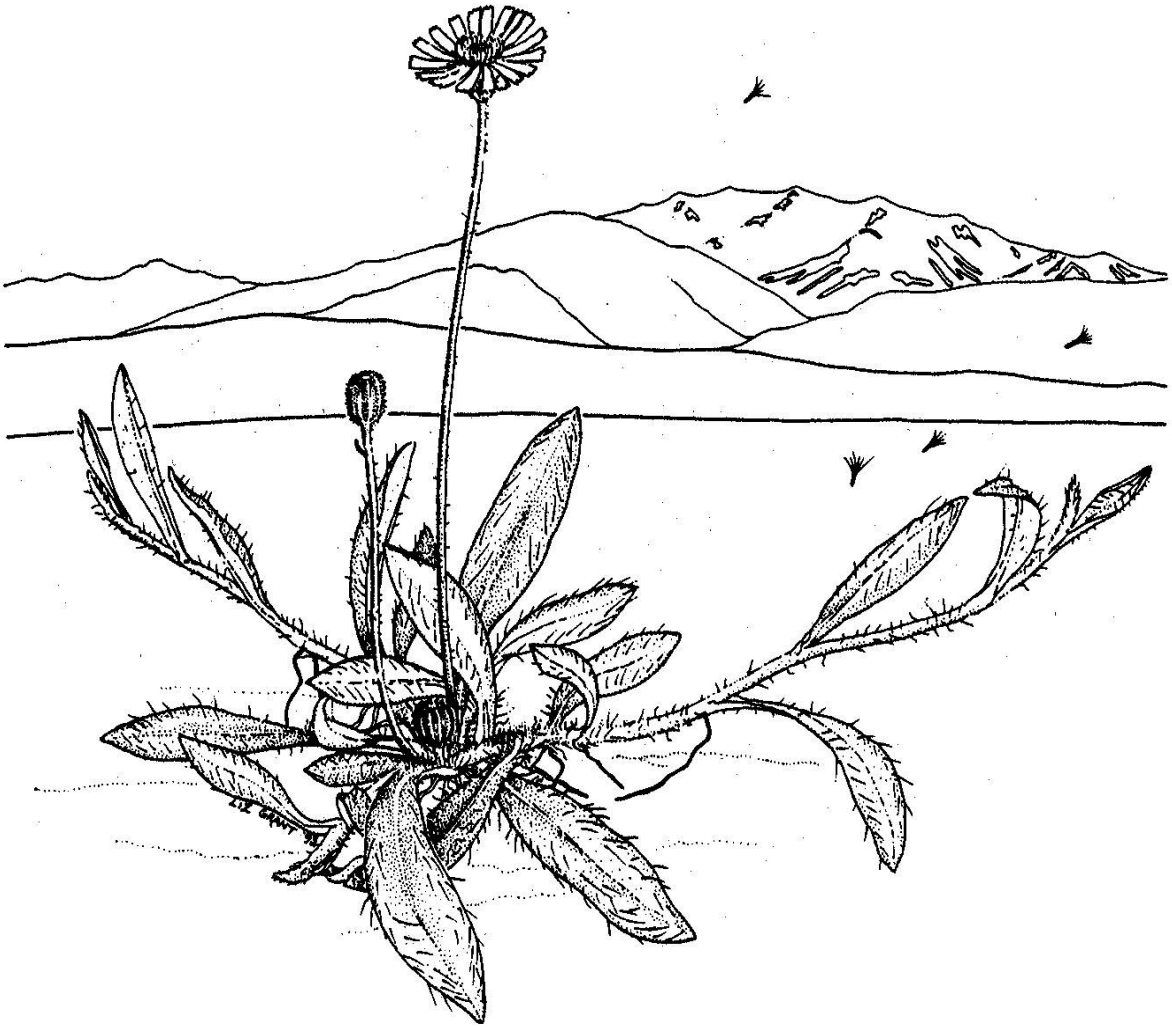

Hieracium pilosella E. A. Grant (1993) cover of NZ J of Ecol 17(1)

Abstract

Hieracium pilosella is an invasive weed of New Zealand's short tussock grasslands. Since the 1960s, the abundance of *H. pilosella* has dramatically increased; it is now thought to occur in 6 million hectares of New Zealand (Espie, 2001), predominantly in grasslands. It is at least common in 42% of this area (Espie, 2001).

Ecology is inherently spatial and as plants closely interact with their direct neighbours, the spatial arrangement of plants is vital to their functioning. A handful of recently published articles have implicated spatial structure of plant communities in theories of plant competition, resource use and the invasion of plant communities. The aims of this thesis were to: 1) determine if there are consistent spatial patterns in New Zealand's short tussock grasslands at relatively small scales (i.e. spatial relationships between individuals); 2) investigate how the invasion of *H. pilosella* may be altering these spatial patterns; and 3) establish if the spatial patterns of species, life-forms and root systems are being altered in different ways.

Spatial patterns of both tussock and inter-tussock species, life-forms and root functional groups were evaluated at a range of short tussock grassland sites across a gradient of *H. pilosella* invasion levels in Canterbury, using both join-count statistics and Ripley's K-function. A classification system for the root functional groups of vascular species in these communities was developed and applied. It was found that species, life-forms and root functional groups in short tussock grasslands had generally consistent spatial patterns across sites both within and between species. These patterns were variable between significantly different levels of *H. pilosella* ground cover. The type of spatial pattern exhibited, and the way it was altered differed between species, life-form and root functional groups. For example, tussocks exhibited increased regularity up to scales of 160 cm and increasing aggregation at scales up to 500 cm, with increases in *H. pilosella* abundance. In contrast, both *Agrostis capillaris* and herbaceous chamaephytes had increased aggregation across scales up to 160 cm. These differences in spatial patterns along the gradient of

invasion are a strong indication that *H. pilosella* is structurally fragmenting New Zealand's short tussock grasslands. This fragmentation is likely to have far reaching effects including the disturbance of invertebrate communities and the disruption of ecosystem services including pollination, vegetation regeneration, and nutrient cycling.

Chapter 1

Introduction

Ecology is inherently spatial (Dale, 1999; Fortin & Dale, 2005). All processes and interactions occurring in an ecosystem have a spatial element. This spatial structure is not only the result of one or more of these processes, but can also have consequences for future processes in the ecosystem. As such, the spatial patterns present in New Zealand's short tussock grasslands are a result of all the current and historic processes occurring within this ecosystem. By examining these patterns we can begin to understand what processes may be important in structuring an ecosystem, and how changes in these spatial patterns may alter current processes.

Hieracium pilosella[1] is a major weed of New Zealand's short tussock grasslands (Espie, 2001), and understanding the effect it is having on the spatial patterns in these ecosystems may indicate how it affects other ecological processes which are important for the sustainability of these grasslands. The spatial patterns of *H. pilosella* itself can also provide clues as to the underlying mechanisms of its successful invasion of these communities.

This thesis begins to examine the spatial patterns of New Zealand's short tussock grassland communities and how these may have been affected by the invasion of *H. pilosella*, focusing on relatively small spatial scales. Its basic approach is to map the vegetation of short tussock grasslands at relatively intensive scales (plots up to 0.04 ha) at various levels of *H. pilosella* invasion, and utilize spatial statistical methods to detect regularity and aggregation in spatial patterns at a variety of small scales (up to 5m). These spatial patterns are then examined for trends along the invasion gradient.

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[1] All nomenclature follows Webb, Sykes and Garnock-Jones (Webb *et al.*, 1988)for naturalised pteridophytes, gymnosperms and dicotyledons; Allan(1961) for indigenous tracheophyta; Edgar and Connor (1966) for grasses; and Moore and Edgar(1976) for other indigenous monocotyledons.

Spatial Plant Ecology

The majority of quantitative ecological studies up until the mid-20th century assumed that there was uniformity within the entire range of an organism (Legendre, 1989); however, from the late 1940s through to the 1960s discussions of the spatial relationships between individuals and species began to appear in the literature, and a variety of spatial statistical methods were proposed (Archibald, 1948; Curtis, 1955; Greig-Smith, 1952; Pielou, 1960; 1961; 1964; Thompson, 1958; Watt, 1947). Ecology based on spatial relationships remained uncommon until the late 1980s, probably due to the extensive complex calculations required for spatial statistics. The increased computational power of modern computers and transfer of improved statistical techniques from other disciplines such as economics and geography probably contributed to the increased interest in spatial plant ecology. Nevertheless, current literature is still dominated by theoretical papers and models, with a paucity of empirical data (Murrell *et al.*, 2001; Stoll & Prati, 2001; Turnbull *et al.*, 2007).

It is now widely acknowledged that spatial patterns are functional and not simply random noise and the study of spatial patterns is termed 'Spatial Ecology' (Legendre, 1993). A wide variety of theories have spatial elements including succession; adaption to environment and evolution; pollination; dispersal; maintenance of species diversity; community stability; competition; predator-prey interactions; parasitism; population genetics; population growth; social behaviour; epidemics, and the effects of natural catastrophes (Legendre, 1989). However, the spatial pattern of a community can only provide inferences (Coomes *et al.*, 1999), not certainty about the processes occurring as several processes may result in similar patterns (Sokal & Oden, 1978) or interact to give confounding patterns (Fortin & Dale, 2005). Spatial patterns can provide imperfect knowledge with which to test hypotheses about processes (Dale, 1999).

Sokal and Oden (1978) recognised four general models for the origin of patterns in ecology: environmental gradients, environmental patchiness, isolation-by-distance, and historical factors such as past disturbance and founder effects. The importance of historical legacies cannot be

underestimated as current patterns may reflect past processes which are no longer operating (Fortin & Dale, 2005). In addition life history traits such as clonal growth and seed dispersal must also be considered (Coomes *et al.*, 1999). In reality these factors work in combination to produce a variety of spatial patterns in vegetation (Coomes *et al.*, 1999; Sokal & Oden, 1978).

With the increasing prevalence of anthropogenic effects on ecosystems, fragmentation is a fundamentally spatial theme of conservation biology which has been intensively studied. Fragmentation occurs when natural or semi-natural habitats are broken up into comparatively isolated patches through human induced disturbance. Generally the concept of fragmentation is discussed at the landscape scale (Saunders *et al.*, 1991), although the concept of structural fragmentation, where fragmentation occurs at very small scales and grain sizes, has been outlined in Lord and Norton (1990) and, McIntyre and Hobbs (1999). Fragmentation has many associated problems including habitat alteration and reduction especially affecting specialists, edge effects, increased vulnerability to disturbance and patchier habitats (Lord & Norton, 1990). The smaller the grain size of fragmentation, the smaller the organisms which may be affected (Lord & Norton, 1990). Both plants and animals may suffer from allee effects, where isolation reduces the number and quality of reproduction opportunities (Weller, 1994); in plants, this is highly dependent on the pollinators and the sexual system of the plant (Wagenius, 2006). Fragmentation may also affect functioning of the ecosystem, interfering with processes, altering nutrient cycling and degrading ecosystem services (Lord & Norton, 1990).

Spatial concepts have also emerged in recent theories of plant competition, resource use and the invasion of plant communities. De Broeck *et al.* (2006) proposed that there is increased vulnerability to invasion where there is clumping of individuals of the same species, as not all resources are utilized and there is niche space available to exotic invasive species. This theory could also explain the biodiversity conundrum, where there are great improvements in ecosystem stability when increasing the biodiversity from a monoculture to biculture, but only small increases

in stability when further increasing biodiversity. In an empirical paper, garden trials undertaken by Stoll and Prati (2001) also indicated that spatial distributions are important to competitive interactions between individuals, and suggested that this importance may occur regardless of the identity of the neighbouring plant or its competitive ability. In addition, Turnbull *et al.* (2007) measured the effect of spatial patterns on competition and found that: 1) all species were aggregated at some level; 2) there were significantly different strengths of association between species and guilds of neighbours; and 3) over two years, the impact of the spatial structure was significantly different between years. All three of these papers suggest that aggregation decreases inter-specific contact and therefore competition between species, which favours species which are relatively poor competitors and allows for greater co-existence. In a related study, it has also been theoretically shown that patchy dispersal resulting in aggregation also allows for long term-coexistence within not just plant associations, but also small water or wind borne animals (Potthoff *et al.*, 2006).

Spatial ecology is still relatively uncommon in New Zealand ecological studies (but see Alspach & Bus, 1999; Cole & Syms, 1999; Duncan, 1991; Duncan, 1993; Duncan & Stewart, 1991; Ettema & Wardle, 2002; McArdle & Blackwell, 1989; O'Driscoll, 1998; Ogden & Lusk, 1992; Reaser *et al.*, 2007; Stewart & Rose, 2001). In a spatial analysis of species in New Zealand's grasslands, Scott (1959; 1961), found that tussocks influenced the zonation of neighbouring vegetation and that each species responds differently. Three possible contributing factors were proposed; the tussocks may modify the surrounding microclimate; tussocks may provide protection from grazing around the base; or the effects of below-ground competition.

Eastern South Island short tussock grasslands

New Zealand's short tussock grasslands are largely composed of *Festuca* and *Poa* species, being relatively short and open vegetation when compared to tall tussock grassland dominated by snow tussocks (*Chionochloa* spp.)(Wardle, 1991). Prior to the arrival of Maori in New Zealand, tussock grasslands were probably only significant in the driest parts of the South Island's inter-montane

basins and frosty valley floors (Mark *et al.*, 2003), where the difficult environment prevented the growth of taller vegetation. It is likely that these areas still had a significant shrub component, depending on the time since the last disturbance (O'Connor & Harris, 1992).

Although there is evidence of widespread fires prior to the arrival of Polynesian people in *ca.* 1280 AD (Wilmhurst, 2007), probably from lightening strikes in a dry climate, most of the burning and deforestation in these areas occurred between the thirteenth and sixteenth centuries (McIntyre, 2007; Rogers *et al.*, 2007). This repeated burning promoted the growth of tussock grasslands which became more widespread (O'Connor & Harris, 1992). These large fires may have occurred for a number of reasons including; encouragement of natural food resources, hunting moa, opening up vegetation to ease transport between the east and west coast, and the escape of domestic fires.

The arrival of European settlers brought with them extensive agriculture. Pastoral use of these areas started in the 1840s (McIntyre, 2007), and sheep numbers peaked in 1878 at 9.5 million (O'Connor & Harris, 1992). The repeated burning of vegetation continued to promote the growth of fresh green grass for grazing. Rabbits were introduced in the 1870s and soon grew to epidemic levels, having a profound and lasting effect on these environments. The introduction of grazing animals, and exotic vegetation by European settlers transformed the environment from predominantly tall tussock grasslands to short tussock grasslands (Treskonova, 1991). Native and overall species richness declined and exotic species richness increased over time (Duncan *et al.*, 2001; Hunter & Scott, 1997; Rose *et al.*, 2004). In 1935, it was estimated that 34% of the South Island, New Zealand was tussock grassland (Hilgendorf, 1935).

This relatively long history (in the context of European settlement in New Zealand), and the close tie between family and land has lead to the South Island high country being highly valued in a social and historical sense (Dominy, 2001). Many of the local families can trace their genealogy to when the land was first settled; and have strong oral and often written histories, and connections to the land (McIntyre, 2007). These areas are also appreciated by others for their unique and

significant scenic and historic values. Although they are highly modified, they are also valued for their biodiversity and ecological values. The current conservation status of the tussock grasslands is good, with 44% of the pre-European settlement grasslands existent, however much of this area has been highly modified. Although the proportion of grasslands legally protected in New Zealand (12.3%) is greater that the international average; most of this area is at high altitudes and low elevation grasslands are poorly represented (Mark & McLennan, 2005).

Short tussock grasslands also have economic value. The majority of income in these areas has traditionally been from the farming of merino sheep for fine wool. This industry was valued at $94 million (2002 real dollars) in 2000/2001(Greer, 2003). The value of tourism from short tussock grasslands has not been quantified; however, the popularity of Queenstown and the Southern Lakes and the Mackenzie Basin must be in part due to the scenic values of the surrounding short tussock grasslands. These grasslands also provide a variety of ecosystem services including collection of water for hydroelectric power generation, maintenance of genetic diversity, and wind soil erosion and loess control.

***Hieracium pilosella*: An invasive weed of New Zealand's short tussock grasslands**

H. pilosella (Asteraceae) is a widely distributed native species in Britain and Europe (Bishop & Davy, 1994), which generally fills a mid-successional niche in dry calcareous grasslands (Degn, 2001). This is only one of nine exotic *Hieracium* species present in New Zealand, with between 5 000 and 10 000 species in the genus worldwide (Espie, 2001)[2]. It was first recorded in New Zealand in 1864, as a localised component of grasslands in Canterbury (Espie, 2001). By the 1960s there were a few records of its presence at a range of sites; however, it was not dominant in these grasslands (Connor, 1992). Since the 1960s, the abundance of *H. pilosella* has dramatically increased; Espie (2001) estimated that it occurred in over 6 million hectares of New Zealand and was at least common or conspicuous in 42% of this area. He also estimated that $45 million

[2] Although, Webb, Sykes and Garnock-Jones (1988) state that there is probably only *ca.* 1 000 good species, with up to *ca.* 5 000 species if apomictic micro-species are included.

dollars had been lost from pastoral production by 1993. In the 15 years since this estimate, it has undoubtedly risen significantly.

The taxonomy of this species is difficult, with between 8 and 624 subspecies (Bishop & Davy, 1994). As is common in the Asteraceae family, it has various levels of ploidy with five cyto-types known world wide (Bishop & Davy, 1994). Two cyto-types are dominant in New Zealand: tetraploid and facultative apomictic pentaploid (Chapman *et al.*, 2003). Analysis of the Chloroplast DNA has indicated that the *H. pilosella* present in New Zealand is likely to be from Eastern Europe with at least four different lineages present (Trewick *et al.*, 2004). This evidence is consistent with the hypothesis that the seed was accidentally introduced with imported grain or grass seed (Jenkins, 1992). There is also evidence in cytometry and chloroplast DNA that there has been complex hybridisation within New Zealand, particularly with *Hieracium praealtum* (Morgan *et al.*, 2004; Trewick *et al.*, 2004).

Due to its impact on tussock grasslands, the invasion of *H. pilosella* into New Zealand has been extensively studied since the 1960s. Several hypotheses for its successful invasion have been given; with a consensus now emerging that it is likely to be combination of factors (discussed below) that are important (Platt *et al.*, 1995). Debate continues as to whether the dominance of this exotic species is a result of, or the cause of degradation to soils and vegetation in New Zealand's high country.

Although *H. pilosella* is found in a range of environments from sea-level to 1500 m asl in both the North and South Islands with 350 to over 3 000 mm mean annual rainfall (MAR); it thrives in relatively low rainfalls of approximately 600 mm MAR, where competition for water is high (Bishop & Davy, 1994; Espie, 2001; Makepeace, 1980). When studying the dry grasslands of Canterbury, Marlborough and Otago, both Walker and Lee (2002) and Duncan, Colhoun and Foran (1997) found that *H. pilosella* decreased in very dry, xeric conditions. There has been a

suggested intolerance of high temperatures from its European distribution (Bishop & Davy, 1994); however the relatively mild climate of New Zealand generally does not show similar gradients.

There is evidence that *H. pilosella* alters the soil nutrient status, reducing the available nutrients and moisture; and producing a halo where the soil remains unoccupied by other vegetation (Boswell & Espie, 1998). The soil under *H. pilosella* is generally more acidic with a higher organic C content and cation exchange than in the halo itself (McIntosh & Allen, 1993; McIntosh *et al.*, 1995; Powell *et al.*, 1997). Scott (2001) also suggests that it may outcompete native plants for mineral nitrogen. *H. pilosella* may also be efficient in absorbing phosphorous, being adapted to soils low in phosphorous, as it responds readily to the addition of sulphur and lime but produces only small responses to the addition of phosphorus in generally infertile soils (Davis, 1997). Strong arbuscular mycorrhizal symbioses have been detected, with the identity of the mycorrhizal species being important to the growth of *H. pilosella* (Grime *et al.*, 1988; van der Heijden *et al.*, 1998).

Another possible hypothesis for its success is the presence of both ecotypes and phenotypic plasticity (Bishop & Davy, 1994). This allows *H. pilosella* to be a "jack of all trades", being competitive in a range of different environments. *H. pilosella* has a complex range of reproductive alternatives ranging from vegetative reproduction to apomixis, self-fertilisation and out crossing. Generally it spreads to new sites through either apomictic or fertilised seed, and then spreads to occupy the site vegetatively (Bishop & Davy, 1984b; Makepeace, 1980; Makepeace *et al.*, 1985; Winkler & Stöcklin, 2002). It has also been found that vegetative reproduction was the dominant mode in grassland populations, however periodic weather dependant flushes of seedling growth occur (Makepeace, 1985b; Winkler & Klotz, 1997). Genetic analysis of New Zealand *H. pilosella* has shown that the level of sexual reproduction and genetic variation varies between sites, and that gene flow may occur between *Hieracium* species or between different cyto-types within *H. pilosella* (Chapman *et al.*, 2003; Chapman *et al.*, 2000; Houliston & Chapman, 2001, 2004). This

mixed reproductive strategy is important for population maintenance when inter-specific competition is high and the abundance of bare ground is low. The seed of *H. pilosella* does not seem to survive long dormant periods and there is no detectable seed bank (Makepeace, 1980)

H. pilosella has been described as a "gap grabber"; rapidly occupying gaps created by disturbance and fluctuating resource availability, but not persisting where there is strong competition by the existing plant communities (Degn, 2001; Rose *et al.*, 1998; Rose *et al.*, 1995; Walker *et al.*, 2005). Also, *H. pilosella* is generally a more successful invader in short open vegetation with greater light availability (Bishop & Davy, 1994; Fan & Harris, 1996; Kohler *et al.*, 2005), and has reduced germination rates under shading which occurs in taller vegetation (Rose & Frampton, 1999). There is evidence of a link between this opportunistic behaviour and increases in *H. pilosella* where there is grazing (Fan & Harris, 1996; Platt *et al.*, 1995; Scott, 1993; Walker & Lee, 2002); however, simply eliminating grazing does not prevent invasion nor improve infested tussock grasslands (Duncan *et al.*, 2001; Ewans, 2004; McIntosh & Allen, 1998; McIntosh *et al.*, 1997; Meurk *et al.*, 2002; Rose & Frampton, 2007; Treskonova, 1991; Walker *et al.*, 2003). *H. pilosella* itself has been described as highly palatable; however, its low stature makes it difficult for medium to large herbivores to feed on. The stems and flower heads may be preferentially grazed when available, (O'Connor & Covacevich, 1992). Although this grazing during flowering may reduce the number of seed heads (Bishop & Davy, 1984b), it has been linked to an increase in stolon number (Makepeace, 1985a) which is the dominant reproductive strategy as previously discussed.

The addition of fertiliser to improve degraded soil quality has also been investigated for the reduction of *H. pilosella*. It is suggested that in specific cases indigenous vegetation may slowly increase in abundance while *H. pilosella* decreases where application of particularly N, P, and S; but also K, lime and micronutrients; is sustained over a long period (Bishop & Davy, 1984a; Norton *et al.*, 2006 ; Rose *et al.*, 1998; Scott, 2001; Scott & Jenkins, 2006). Short bursts of only one or a few years fertilisation alone is insufficient to improve the abundance of slow growing

native species, however when combined with the over sowing of fast growing species, may result in a reduction in *H. pilosella*. This type of management is counter-productive where indigenous biodiversity values are important (Moen & Meurk, 2001; Scott, 1993, 2000; Scott *et al.*, 1990a).

A lack of natural predators in New Zealand has also been cited as a possible contributing factor to the successful invasion of *H. pilosella*, and bio-control has been suggested as a possible management technique. *H. pilosella* has few specific parasites in New Zealand which effect its reproduction despite a wide variety of naturalized and native insects found utilizing the plants (Syrett & Smith, 1998). A suite of both insects and rust fungi have been introduced into New Zealand with the hope of assisting to control the species; however, none are yet to be universally useful (Jenkins, 1995).

Weigelt *et al.* (2007; 2002) investigated the relative importance of plant size and species identity to plant competition using species from European grasslands, including *H. pilosella*. They found that species identity was the most important factor when determining the effects of competition, with a species specific plant size factor playing a non-additive role. The competitive interactions between a variety of exotic and native grassland species and *H. pilosella* in New Zealand have been investigated using pot trials. Generally there has been a lack of specific competitive effects against *H. pilosella* (Moen & Meurk, 2001; Scott & Sutherland, 1993), although Makepeace (1985) did detect some interference of *Festuca novae-zelandiae* on *H. pilosella*. *H. pilosella* has a variable but consistently negative effect on *F. novae-zelandiae*, *Raoulia australis* and *Acaena buchananii*, with the tussock species being its strongest competitor. The height of the tussock is thought to be the driving factor behind this competition (Moen & Meurk, 2001). Fan and Harris (1996) found that the addition of fertiliser, making the environment more favourable, increased interference between *H. pilosella* and three other species.

Whether *H. pilosella* has an allelopathic (chemical inhibitory) affect on other species has been widely debated and investigated; however, it is yet to be conclusively proved or disproved.

Possible allelopathic chemicals from both the leachate of dead leaves and roots have been detected, particularly umbelliferone, caffeic acid, chlorogenic acid, apigenin-glucoside and mannitol (Henn *et al.*, 1988; Jenkins, 1992; Makepeace, 1980; Orchard, 1993). Free aluminium under *H. pilosella* patches has been detected at levels which would affect red clover and other New Zealand high country species; however the link between *H. pilosella* and free aluminium is unclear (Powell *et al.*, 1997). In pot and field trials, there has been few detectable effects in adult plants (Henn *et al.*, 1988; Orchard, 1993; Scott & Sutherland, 1993); however, some species specific effects have been detected in seed germination (Makepeace *et al.*, 1985). These effects are likely to be irregular and transitory (Makepeace, 1980; Wiedera, 1978) perhaps being more common where there is plentiful autumn rain after a dry summer so that water percolates through dead dry leaves, and greater in harsh environments (Jenkins, 1992). Auto-intoxication has been detected, with rosettes on the edge of patches being more vigorous than central ones which may be due to similar allelopathic effects (Bishop & Davy, 1994; Wiedera, 1978).

Spatially, rosettes of *H. pilosella* in Europe can be thinly and uniformly scattered, present in small clustered groups or present in large thick aggregations ranging from 600-1200 rosettes per square meter, up to a maximum of 3000 (Bishop & Davy, 1994). Similar spatial studies of New Zealand's populations have not been undertaken.

Thesis objectives and structure

The aims of this thesis are to: 1) determine if there are consistent spatial patterns in New Zealand's short tussock grasslands at relatively small scales; 2) investigate how the invasion of *H. pilosella* may be altering these spatial patterns; and 3) establish if the spatial patterns of species, life-forms and root systems are being altered in different ways.

Following this introductory chapter, which contains literature reviews of spatial plant ecology, New Zealand's short tussock grasslands and the ecology of *H. pilosella,* chapter 2 describes in detail the study sites used in this thesis. Chapters 3, 4 and 5 are all written as autonomous journal

articles which have been or will be submitted to peer-reviewed journals for publication, as such there may be some repetition of literature review (Chapter 1) and study site descriptions (Chapter 2). Chapter 3 addresses changes in the spatial patterns of tussocks with the invasion of *H. pilosella.* Chapter 4 proposes an updated functional classification of grassland plants based on their root systems. Chapter 5 looks at the spatial patterns of inter-tussock species and life-forms along the gradient of *H. pilosella* invasion, and incorporates the classification system proposed in chapter 4 to investigate the spatial patterns of various root functional groups. The final chapter (6) brings together the results and themes of the previous chapters and draws overall conclusions for this thesis.

Chapter 2

Study sites

The eastern South Island

For this thesis, a range of sites within Canterbury, eastern South Island were selected for study. Canterbury has a varied environment and geology. The movement and uplift of the Pacific and Indo-Austral tectonic plates has created the backbone of the South Island; the Southern Alps (Wardle, 1991). The eastern side of the Southern Alps north of Otago is made up of Mesozoic sedimentary greywacke lifted from the ocean floor (Wardle, 1991). At lower altitudes, the surface rocks are tertiary and quaternary sedimentary rocks (Wardle, 1991) with plains formed from alluvial depositions and loess. Large glaciers during the Holocene formed large U-shaped valleys and inland basins (Gage, 1969). The soils of Canterbury are as varied as the geology, reflecting the landforms of the area (Vucetich, 1969)

The climate of Canterbury is dictated by prevailing westerly winds and the dominance of the Southern Alps along the western boundary (Ryan, 1987). Orographic rainfall patterns caused by clouds from the west releasing their moisture as they rise and move over the Alps, mean that there is a steep gradient of rainfall across Canterbury. The areas around the ranges and hill country receive significantly more precipitation than the plains and coastal areas in the east of Canterbury (de Lisle, 1969; Ryan, 1987). Strong nor' westerly föhn winds, which are warm and dry after flowing across the hills and plains, aren't frequent but they are an important influence on Canterbury's climate (de Lisle, 1969; Ryan, 1987). Canterbury is warmest in January and February and coldest in July with an overall mean annual temp for Canterbury around 11°C (de Lisle, 1969). The daily temperatures vary 11-12°C on the inland plains and hill country, but probably only around 5-7°C in some montane areas (Ryan, 1987), and ranges more in summer than winter (Ryan, 1987). The occurrence of frost varies across the region with frosts possible in all seasons in the high country; however, coastal areas around the Banks Peninsula northwards may have frost free years (Ryan, 1987).

808,000 hectares of Canterbury's mountains, forests and tussock grasslands forms part of New Zealand's conservation estate which is managed by the Department of Conservation[3] primarily for conservation purposes. The majority of the remaining land is managed privately, whether through Crown Pastoral Lease or freehold ownership, in a mixture of urban and rural land uses.

The following description of Canterbury's current vegetation has been derived from Wardle (1991) and Knox (1969). The native forests of Canterbury are largely restricted to the hills and mountain slopes, being fragmented remnants of pre-human forests which would have cloaked much of the region. At low altitudes near the coast these remnants are characterised by matai (*Prumnopitys taxifolia*), kahikatea (*Dacrycarpus dacrydioides*), totara (*Podocarpus totara*) and mixed angiosperm trees and shrub species; however, beech (*Nothofagus* spp.), particularly mountain (*Nothofagus solandri* var. *cliffoidies*) and black beech (*Nothofagus solandri* var. *solandri*) from Arthurs Pass northwards, dominate in inland areas near the ranges, where the rainfall is higher and the soils more infertile. Hall's totara (*Podocarpus hallii*) forms an important part of remnants on drier sites, and grows mixed with Kaikawaka (*Libocedrus bidwillii*), pink pine (*Halocarpus biformis*) and *Phyllocladus alpinus* south of Arthurs Pass, and grows with a diversity of angiosperm shrubs and small trees. Exotic conifer forests, mainly *Pinus radiata* and *Pseudotsuga menziesii*, have been planted since the settlement of Europeans on the hills and plains in Canterbury, with wildings becoming a problem in some areas, including the Mackenzie Basin and areas of the High country. Tall heaths and subalpine bush dominated by *Dracophyllum* spp., snow totara (*Podocarpus nivalis*), *Phyllocladus alpinus* and Hall's totara form remnants which grade into grasslands and forests in the heads of remote valleys. Characteristic Grey Scrub, which is a mixture of *Coprosma* spp., *Aristotelia fruticosa*, *Corokia cotoneaster* and matagouri (*Discaria toumatou*), along with other shrubs, is common across the rainfall gradient (400-6 000mm). In moist lowland valleys, Grey Scrub is seral to forest; but forms a patchy mix with tussock grasslands as an edaphic climax in the driest inland districts. Tall tussock grasslands, dominated

[3] http://www.doc.govt.nz/templates/defaultlanding.aspx?id=32205

by *Chinochloa* spp., of subalpine zones and wet valley floors are seral, tending to be invaded by taller shrubs and grey scrub species. The short tussock grassland communities, including those which are investigated in this thesis, are common in the inland basins and valleys of Canterbury. They are made up of several tussock species, but are most commonly dominated by *F. novae-zelandiae* and have probably expanded their distribution since pre-human times as repeated fire and grazing have allowed them to spread from dry areas, frosty flats and disturbed sites. At lower altitudes, on the foothills and plains of Canterbury, crops and exotic grasses for domestic grazing dominate the vegetation and are the dominant land cover in Canterbury today.

Specific study sites

The following study sites (Figure 1) were chosen as they are all *F. novae-zelandiae* short tussock grasslands located in Canterbury, with low management inputs. Although all of the sites are subjected to some grazing by exotic mammal herbivores (domestic or feral), none have high management inputs as they have not been over sown, top dressed, fertilised or irrigated. They represent a range of invasion levels of *H. pilosella*, ranging from sites with very low levels to those which have been inundated and are dominated by *H. pilosella*. Effort was made to use study sites with similar climates, landforms and edaphic variables; however this was difficult, as the level of *H. pilosella* invasion is strongly correlated to environmental factors. The landowners of all of these sites were also comfortable with non-destructive data collection being undertaken on their land.

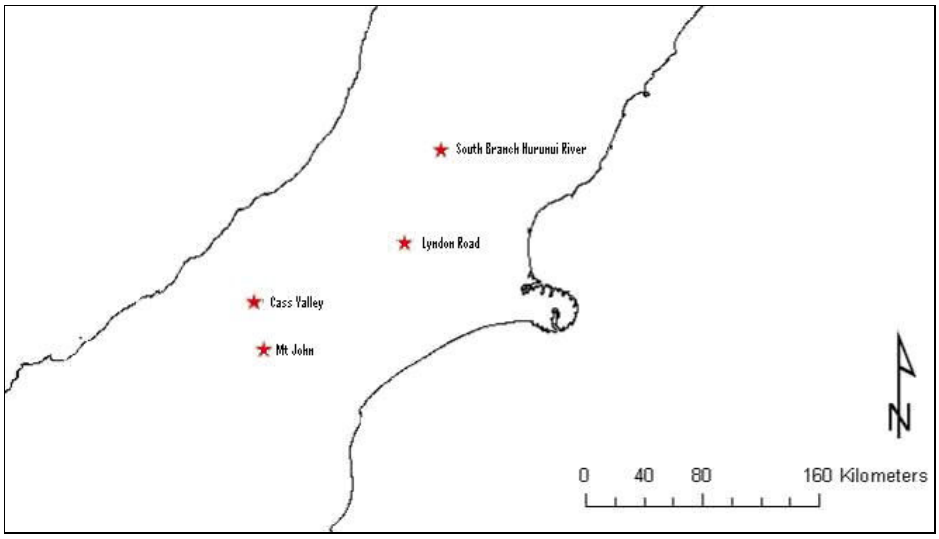

Figure 1 Map of study site locations

Mt John Agreasearch Trials

Figure 2 General photo of Mt John study site, looking south-east

The Agresearch Trials at Mount John, west of Lake Tekapo in the Mackenzie Basin, were established in 1982 (Scott, 1999) to examining various aspects of grazing, fertilizer, irrigation and over sowing in relation to agricultural outputs. The specific study site (Figure 2) utilized in this thesis is situated adjacent to the trial plots to the North.

The site is a gently rolling moraine, 760 m above sea level (Land Information New Zealand, 1997), with soils formed from the greywacke and argillite till overlain with loess since the last glacial retreat 13,000 years ago (Scott, 1999). These Tekapo Soils consist of fine sandy loams are

generally shallow and stony with medium fertility. Soil tests undertaken for this study show that these soils are acidic (pH 5.4-5.7), with low Olsen soluble P (12-18 μg/mL), and low organic (2 μg/g) and inorganic S (4 μg/g), but moderate N levels (0.32-0.42 %w/w). They are prone to wind erosion in areas with poor vegetation cover and high winds (Soil Bureau, 1963). There has been no addition of fertiliser, irrigation or over sowing to the area generally, although specific trials do contain these treatments (Lamoureaux, 1998).

The climate is sub-humid, receiving only 600 mm mean annual rainfall (New Zealand Meteorological Service, 1985) which is generally uniform throughout the year with a slight decrease in February and March (Scott, 1999). This is the driest of the study sites, with an annual water deficit of 273 mm (LandcareResearch, 2003) (Table 1). The variation in temperature is greatest over the summer months (Scott, 1999).

The Mt John site was first grazed by sheep in the 1860s (Scott, 1999) and in 1963 vegetation surveys at Mt John indicated that *H. pilosella* had an erratic or sparse presence (Connor, 1992). Currently the study site's vegetation consists of highly invaded *F. novae-zelandiae* short tussock grassland dominated by *H. pilosella*. *H. pilosella* has apparently reached equilibrium at this site, with density dependent mortality and density independent reproduction regulating the population (Lamoureaux, 1998). Other monocotyledonous and dicotyledonous inter-tussock species make up a small proportion of the cover.

A more detailed description of this study site can be obtained from Scott (1999).

Table 1 Selected study site environmental and climatic statistics

Study Site	South Branch Hurunui River	Lyndon Road	Cass Valley	Mt John
Location	42°45'50"S 171°59'12"E	43°20'19"S 171°40'35"E	43°40'34"S 170°22'49"E	42°45'50"S 171°59'12"E
Altitude	840 m asl	835 m asl	1080 m asl	760 m asl
Distance from main divide (to the nearest 5km)	10 km	50 km	20 km	50 km
Landform	Alluvial terraces	Alluvial terraces	Alluvial terraces	Gently rolling moraine
Mean annual rainfall§ Annual water deficit‡	2400 mm 0	1200 mm 0	3000 mm 0	600 mm 273 mm
Mean annual temperature‡	7.9°C	8.2°C	7.0°C	8.5°C
Mean minimum daily temperature of the coldest month‡	-2.2°C	-1.6°C	-2.4°C	-2.5°C
Mean annual solar radiation‡	13.6 MJ/m^2/day	13.8 MJ/m^2/day	14.2 MJ/m^2/day	14.6 MJ/m^2/day
Chemical limits to plant growth‡*	1	1	1	1
Drainage ‡†	5	5	5	5

§ interpolated from climatic maps (New Zealand Meteorological Service, 1970) , ‡ derived from the underlying data of LENZ (LandcareResearch, 2003), * 1 = low, 2 = moderate, 3 = high,† 1 = very poor, 2 = poor, 3 = imperfect, 4 = moderate, 5 = good/well

Cass Valley

Figure 3 Photo looking down Cass Valley (south) across the study site.

The Cass Valley site (Figure 3) is situated on alluvial flats at the confluence of Alisa Stream and Cass River which then flows into the Mackenzie Basin. Alisa stream has strong colluvial influences with an active river bed of angular gravel, while the Cass Valley has a gently sloping braided bed; both valleys have been extensively glaciated in the past. At 1080 m above sea level (Land Information New Zealand, 1998a), the area is not far from the main divide of the South Island, and therefore has strong sub-alpine influences on both vegetation and climate.

The soils of this area form part of the Kaikoura Steepland Soil Series with silt, sand and stony loams formed from greywacke and greywacke detritus parent material. These soils have very low fertility and are subject to severe wind, sheet, scree and gully erosion, particularly where the soil is vulnerable to the affects of frosts (Soil Bureau, 1963). There has been no fertiliser addition, irrigation or over sowing under taken in this area. Soil tests carried out for this study show that these soils are variable but acidic (pH 5.4-6.0), with very low Olsen soluble P (6-10µg/mL), and low organic (1-4µg/g) and inorganic S (2-9µg/g), and greatly variable N levels (0.12-0.62 %w/w).

The annual rainfall is significantly higher than the Mt John site (Table 1) due to its proximity to the main divide and the strong orographic rainfall shadow which is exhibited across the South Island of New Zealand. It is estimated that the mean annual rainfall of the study site is approximately 3000mm (LandcareResearch, 2003). The mean annual temperature is lower than Mt John, at 7.0°C, but they have similar mean minimum daily temperatures in the coldest month (Table 1).

The land is managed by Glenmore Station under a Crown Pastoral Lease, as part of their summer grazing run. As such it hasn't had any over sowing or fertilisation, and receives only light grazing from both sheep and cattle in the summer months.

The vegetation types represented at the study site include; *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland on drier sites, *Agrostis capillaris* dominated *F. novae-zelandiae* short tussock grassland where greater soil moisture is available, and small areas of *Poa novae-zealandiae* dominated short tussock grassland on more recent colluvial soils. Generally the inter-tussock space is dominated by either *H. pilosella* or *A. capillaris*, however other species present include*; Pimelia oreophilla*, *Leucopogon fraseri*, *Raoulia* species, *Wahlenbergia albomarginata*, non-vascular mosses, *Anthoxanthum odoratum*, mat *Coprosma* spp. and *Trifolium repens*.

Lyndon Road

Figure 4 Photo looking west across Lyndon Road Study site; tussock grasslands in the foreground

The third study site (Figure 4) is situated on Lyndon Road which connects Lake Coleridge to Lake Lyndon in inland mid-Canterbury. The study site is situated on the eastern side of Lyndon Road, approximately half-way between the lakes, on flat to gently sloping high terraces 835m above sea level (Land Information New Zealand, 1998b).

The Craggieburn soils of the area are silt to sandy loams from greywacke loess parent material over gravels. The generally very low to low fertility soil is susceptible to severe wind erosion where the soil is exposed to frosting (Soil Bureau, 1963). There has been no addition of fertilizer, irrigation or over sowing in this area. Soil tests undertaken for this study show that these soils are acidic (pH 5.2-5.3), with low Olsen soluble P (8-13µg/mL), and low organic (3µg/g) and inorganic S (8-15µg/g), and moderate to high N levels (0.40-0.65 %w/w)

The climate is moderately moist with approximately 1200 mm of rain recorded annually (New Zealand Meteorological Service, 1970)(Table 1), with no annual water deficit (LandcareResearch, 2003). The extreme temperatures are more moderate than the other three sites, only dropping to -1.6°C mean minimum daily temperature of the coldest month.

The land is managed by the Department of Conservation, as part of the Korowai/Torlesse Tussocklands Park. As such it is not actively grazed by domestic stock or over sown and fertilised; although, it does have a grazing history prior to park establishment.

Vegetation surveys in the nearby Archeron River area (820 m asl) in 1964 recorded *H. pilosella* as absent and *Hieracium praealtum* present but erratic (Connor, 1992). Today, *Hieracium* species still have a relatively low abundance in the area, with tussock grassland areas are dominated by *F. novae-zelandiae*, browntop (*A. capillaris*) and other exotic grass species. The slopes above the terraces have a cover of shrubs with tussock grasslands on ridges, and a few forest remnants in the heads of gullies.

South Branch Hurunui River

Figure 5 Photo of South Branch, Hurunui River study site

The alluvial flats of the South Branch of the Hurunui River (Figure 5), 840 m above sea level (Land Information New Zealand, 2001), are one of the few sites of *F. novae-zelandiae* short tussock grassland in New Zealand which has not been overwhelmingly invaded by *H. pilosella*. The relative isolation of this area and lack of recent farming history has most likely protected the area from the arrival of *H. pilosella* seed dispersal, however its presence appears to have increased since Walker and Lee's (2002) survey.

These flats are dominated by recent soils of the Tasman soil series, which are sandy and silty loams from greywacke alluvium parent material, and have medium to low fertility. These soils are subject to stream erosion and deposition of coarse detritus due to their close proximity to active river beds (Soil Bureau, 1963), as a consequence, the soils are variable and at times very thin. Soil tests carried out for this study have indicated that these soils are acidic, with a pH between 5.2 and 5.7, with low Olsen P (8-18), organic and inorganic S (2-5 and 1-5 respectively). The total N was variable, ranging from 0.13 (low) to 0.81 (high). The C/N ratio ranges between 10 and 14, which is normal for agricultural soil.

Due to its proximity to the main divide and the strong orographic rainfall effect, the climate of the South Branch Hurunui River is moist, receiving 2400 mm mean annual rainfall (Table 1)(New Zealand Meteorological Service, 1970), with no annual water deficit (LandcareResearch, 2003). It has a mean annual temperature of 7.9°C (LandcareResearch, 2003), which is similar to all three other study sites.

There has been no development of this land for agricultural purposes, with no addition of fertiliser, irrigation or over sowing. The land is currently managed by the Department of Conservation as part of a mainland island reserve and as such mammalian predators are controlled; however, hares are common on the alluvial flats and are likely to have a significant grazing effect.

The vegetation of the South Branch of Hurunui River is the most intact of all the study sites. The valley walls are cloaked in a closed canopy of beech forest to the tree-line, with native alpine vegetation above this where the mountain ranges exceed the tree-line. The valley floor consists of alluvial flats of various ages, from recent alluvial braided river bed to *F. novae-zelandiae* short tussock grasslands. The exotic component of these grasslands is relatively low when compared to the other three study sites, with small amounts of *H. pilosella,* exotic grasses and annuals.

Chapter 3

Spatial patterns of tussocks in New Zealand's *Hieracium pilosella* invaded short tussock grasslands

Summary

Because plants closely interact with their direct neighbours, the spatial arrangement of plants is vital to their functioning. *Hieracium pilosella* is an invasive weed of New Zealand's short tussock grasslands which is likely to be structurally fragmenting the indigenous flora and fauna. All tussocks within fifteen plots from a range of sites across a gradient of *H. pilosella* invasion were mapped, and Ripley's K-function used to determine their pattern of aggregation and regularity in scales up to 500 cm. The size class distribution of *F. novae-zelandiae* was found to be unrelated to the estimated cover of *H. pilosella*. Statistically significant trends of decline in *F. novae-zelandiae* and overall short density with increases in *H. pilosella* were detected. Also, a significant trend of increased aggregation at moderate scales in *F. novae-zelandiae* with increases in *H. pilosella* cover was found ($P = 0.03$). This increase in aggregation is probably the result of the tussock species being outcompeted by the invasive *H. pilosella* and retreating to refugia microsites. This will have flow on effects for other inter-tussock species and the continuing invasion of *H. pilosella*.

Introduction

Spatial patterns in ecosystems are the sum of all past and present ecological processes and have implications in a wide range of ongoing processes including succession, adaption to environment and evolution, pollination, dispersal, maintenance of species diversity, community stability, competition, predator-prey interactions, parasitism, population genetics, population growth, social behaviour, epidemics, and the effects of natural catastrophes (Legendre, 1989). This is especially true in plants because immobile individuals interact primarily with their direct neighbours (Silvertown *et al.*, 1992).

Spatial concepts have emerged in recent theories of plant competition, resource use and the invasion of plant communities. In garden trials undertaken by Stoll and Prati (2001), spatial distributions were found to be important to competitive interactions between individuals. Intra-specific aggregation was found to decrease inter-specific contact and therefore competition between species, which favours species that are relatively poor competitors and allows for greater co-existence. Turnbull *et al.* (2007) measured the affect of spatial patterns on competition in a field trial and found that 1) all species were aggregated at some level; 2) there were significantly different strengths of association between species and guilds of neighbours; and 3) the effect of spatial relationships on the outcome of competitive interactions was significantly different between two years. De Broeck *et al.* (2006) proposed increased vulnerability to invasion where there is clumping of individuals of the same species, because not all resources are utilized and niche space is available for exotic invasive species. They suggest that this observation could also explain the biodiversity conundrum, where there are great improvements in ecosystem stability when increasing the biodiversity from a monoculture to biculture, but only small increases in stability when further increasing biodiversity. A monoculture is made up of individuals who utilise similar resources in similar ways, and all other resources remain available for use. By increasing the biodiversity to a mixed biculture there are now two types of individuals which utilise resources in two different ways complementing each other's resource use and greatly reducing the remaining untapped resources which remain available for use. When increasing bio-diversity further fewer untapped resources remain; however, the gains are smaller because both the resources and the different ways life can utilise them are limited and niche overlap occurs.

H. pilosella is an invasive weed of New Zealand's tussock grasslands, predominantly affecting the drier areas of the eastern South Island hill and high-country grasslands (Espie, 2001). It was accidentally introduced from Europe prior to 1864, but has only become a significant and

widespread problem since the 1970s (Espie, 2001). *H. pilosella* has significantly impacted both agricultural and ecological values of these tussock grasslands.

The invasion of exotic species is known to have a variety of effects on indigenous species including extinction by hybridisation, habitat alteration and destruction, changes in ecosystem functioning, and fragmentation (Reaser *et al.*, 2007). Fragmentation is the physical isolation of individuals or remnant communities and interferes in a range of ecosystem processes such as dispersal and reproduction. Lord and Norton (1990) coined the term "structural fragmentation" for fragmentation which occurs on small spatial scales, isolating individuals within the community. The small grain size of structural fragmentation implies that it may affect even the smallest organisms (Lord & Norton, 1990; McIntyre & Hobbs, 1999). It is hypothesised that the invasion of *H. pilosella* has caused this kind of fragmentation in New Zealand's short tussock grasslands.

Scott (1959; 1961) found that prior to the invasion of *H. pilosella* tussocks influenced the zonation of neighbouring vegetation and that each species responded differently to the tussocks. Three possible contributing factors to this pattern of zonation were proposed; tussocks modify the surrounding micro-climate; tussocks provide protection from grazing around their base; or there may be spatial effects of below-ground competition. However, Scott (1959; 1961) did not look at the spatial patterns of the tussock species themselves and little is known about their small scale spatial relationships. Lord (1992; 1993) studied the spatio-genetic relationships of *Festuca novae-zelandiae* using isozyme electrophoresis and found that the fragmentation of a single tussock into separate smaller tussocks may contribute to tussock regeneration; however, this is unlikely to be important to the regeneration of the grasslands as a whole. However, there have been no studies of the spatial patterns of tussock grasslands with regard to the invasion of *H. pilosella*.

This chapter focuses on the spatial relationships of *F. novae-zelandiae* across a gradient of *H. pilosella* invasion. It is hypothesised that: 1) *F. novae-zelandiae* will have a unique spatial pattern

of aggregation and regularity across a range of spatial scales that is common to this species at similar sites, and 2) that this unique spatial pattern will be altered by the invasion of *H. pilosella*. If those predictions are true, then the alteration in spatial patterns provides evidence of the importance of spatial structure to competition and invasion biology, and also implies that there may be flow-on effects for other species in this community, both floral and faunal.

Study Sites

It was not possible to locate environmentally similar sites with a range of *H. pilosella* invasion levels because generally in Canterbury the only short tussock grassland sites with low or no *H. pilosella* invasion are in cooler locations with relatively high mean annual rainfalls (Walker & Lee, 2000, 2002). As a result the four sites studied here; South Branch of Hurunui River, Lyndon Road, Cass Valley and Mt John; have disparate climates (described below). However, all of the sites are similar in that they are *F. novae-zelandiae* short tussock grasslands with grazing of either domestic stock or feral hares, very little or no slope, generally good drainage, low fertility and no history of fertilisation

South Branch of the Hurunui River is one of the few sites of *F. novae-zelandiae* short tussock grasslands which are not significantly invaded by *H. pilosella* (Walker & Lee, 2002) . Its proximity to the main divide of South Island means that it is subject to a strong orographic rainfall effect and high mean annual rainfalls (Table 1). The cool moist climate, relative isolation, and lack of farming history have probably protected this area from the invasion of *H. pilosella*; however, its presence seems to have increased since Walker and Lee's (2002) survey . The alluvial nature of these grasslands means that the soils can be very thin in places. Because this area is under the management of the Department of Conservation, it is not actively managed for grazing; however feral hares do have an impact on the flats.

Lyndon Road connects Lake Coleridge to Lake Lyndon in inland Canterbury. The study site itself is situated on the eastern side of Lyndon Road; approximately half-way between the two lakes on flat to gently sloping terraces and receives moderate mean annual rainfalls with cool temperatures (Table 1). *A. capillaris* dominates the *F. novae-zelandiae* tussock grassland with low levels of *H. pilosella*. This area is also managed by the Department of Conservation, without active management for grazing, although it has been grazed in the past by sheep and cattle.

The Cass Valley study site is located at the confluence of Alisa Stream and Cass River, comprising of alluvial flats. Similar to the South Branch of Hurunui River, this site's higher altitude and closer proximity to the main divide of South Island means that it has higher orographic rainfall (Table 1). The vegetation is *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland but with localised *A. capillaris* on damper soils. This site forms part of a summer grazing block for Glenmore Station, receiving light grazing of both sheep and cattle in the summer months.

Mt John, located west of Lake Tekapo, is a gently rolling moraine with a sub-humid climate (Table 1). The site's vegetation is a *H. pilosella* dominated *F. novae-zelandiae* short tussock grassland. It has a long history of sheep grazing and is adjacent to an AgResearch experimental trial established in 1982 examining the effects of grazing, fertilizer, irrigation and over-sowing on a *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland (Scott, 1999); however, the specific study area has not received any of these treatments.

Materials and Methods

Fifteen square plots with $4m^2$ subplot grids, ranging from 100 m^2 to 400 m^2 were established at the four sites (Figure 6); five at Cass Valley, four each at Mt John and South Branch Hurunui River, and two at Lyndon Road. This range in plot size was due to the variation in tussock density; sites were the tussocks were dense required greater time and effort to measure than those sites where the tussocks were sparser and the smallest plots took up to 18 hours to measure. Because spatial

statistics generally assume stationarity; i.e. the spatial distribution of any set of samples is independent to the sample's specific placement (Dale, 1999; Fortin & Dale, 2005); plots were located psuedo-randomly on flat and even terrain, with an even distribution of vegetation to ensure there were no obvious environmental gradients within the plot. The cover abundance of all vascular species was visually estimated within each plot using five cover classes (1 = <1%, 2 = 1-10%, 3 = 11-33%, 4 = 34-66%, 5 = >66%); and two perpendicular basal diameter measurements were made for each short tussock (*Poa colensoi* and *F. novae-zelandiae*) within the plot. The basal area of each tussock was calculated, based on an elliptical surface area. All tussocks within the plot also had their position mapped using a coordinate system to the nearest centimetre. Because *F. novae-zelandiae* is known to reproduce vegetatively by rhizomes (Lord, 1992), a single tussock was regarded as being physically separate from others at ground level if the gap was greater than one centimetre. In total, *ca.* 17,000 tussocks were measured and mapped across the 15 plots.

Figure 6 Photo of Plot 10 (Cass Valley), showing the layout of 2m^2 grids

Plot cover abundance data were classified using the polythetic divisive technique of indictor species analysis (Hill *et al.*, 1975) in winTWINS 2.3 (Hill & Šmilauer, 2005). The five cover

abundance classes described above were used as cut levels with no added weightings and a maximum of 7 divisions. All other default options were used.

Spearman's rank correlation coefficient was calculated in R (R Development Core Team, 2006) for relationships between both the *H. pilosella* and combined *A. capillaris* and *H. pilosella* cover, and tussock density, total basal area per hectare and plot mean height of both *F. novae-zelandiae* and all short tussocks (*F. novae-zelandiae* and *P. colensoi*).

In order to examine the effect of *H. pilosella* on the demographics (as inferred from tussock size) of the tussock population, size class frequency histograms of the individual *F. novae-zelandiae* tussock basal areas in each plot were constructed, with 50cm size classes, and a reverse J-curve fitted ($y=ax^{-3/2}$). The fit of these reverse J-curve models to the measured size class frequencies was tested using R^2 values.

The spatial patterns of *F. novae-zelandiae* and all short tussock species in each plot was determined for scales up to 500 cm using Ripley's K-function (*K(t)*) (Cressie, 1993; Dale, 1999; Diggle, 2003; Fortin & Dale, 2005; Ripley, 1981; 1988) in MATLAB 7.0(Martinez & Martinez, 2002; The MathWorks Inc., 2004), with an isotropic edge correction (Goreaud & Pélissier, 1999; Hasse, 1995; Ripley, 1988) and Monte-Carlo analysis (100 binomial simulations) to produce upper and lower envelopes ($\alpha=0.02$) (Appendix 1) (Goreaud & Pléssier, 2003; Griffith, 1988). In brief, Ripley's K-function counts the mean number of tussocks within a specified distance of every tussock and compares this against what would be expected if the pattern was completely spatially random at the same overall density. Ripley's K-function (*K(t)*) was transformed using Goreaud transform ($L(t) = \sqrt{K(t)/\pi} - t$) before being plotted against the scale of pattern (t), in order to clearly visualise Ripley's K-function over the full range of scales (Figure 11). Where the measured *L(t)* (solid line) is greater than the upper envelope (broken line) the tussocks are aggregated more than expected with a random pattern at that scale, and where the measured *L(t)* is smaller than the lower

envelope (broken line) the tussocks form a regular pattern. Where the measured *L(t)* falls between the upper and lower envelope, the pattern is not significantly different from being completely spatially random. For each plot this produced a trait of either regularity, aggregation, or not significantly different from spatially random; independent of the plot's tussock density for each centimetre scale between 0 and 500 cm. Unweighted pair group method (UPGMA) hierarchical clustering with Jaccard's coefficient of similarity utilising these traits was then used to group the plots into similar spatial patterns in MATLAB 7.0 (The MathWorks Inc., 2004). As there were only 15 plots measured, the non-parametric Wilcoxon rank sum test was implemented in R (R Development Core Team, 2006) to compare the level of *H. pilosella* invasion amongst the different groups of spatial patterns. A significant *P*-value ($P<0.05$) indicates that there are significant differences in the level of *H. pilosella* between different types of spatial patterns.

Results

Although all plots measured were clearly *F. novae-zelandiae* short tussock grassland, the divisive indicator species analysis using WinTWINS 2.3 classified the plots into groups from the same sites, indicating that differences in vegetation composition is greatest between sites, rather than between plots at the same site (Figure 7) . The Cass Valley site is the only exception to this, with the plots divided into two groups at the second division and half of the plots most similar to Lyndon Road with high exotic pasture grasses (*Anthoxanthum odoratum* and *A. capillaris*) and low or no *H. pilosella*; and the other half of the plots most similar to Mt John with only moderate exotic pasture grass and high *H. pilosella* cover (Figure 8). This analysis also shows that the South Branch of the Hurunui is considerably different from the other three sites, being separated from all of them at the first division with low ground covers of both *H. pilosella* and exotic pasture grasses. Species which are present in similar quantities across all of the sites include *F. novae-zelandiae* (the dominant tussock), *Wahlenbergia albomarginata, Leucopogon fraseri* , *Brachyglottis bellidioides, Hieracium praealtum*, *Geranium sessiliflorum* and *Luzula rufa.*

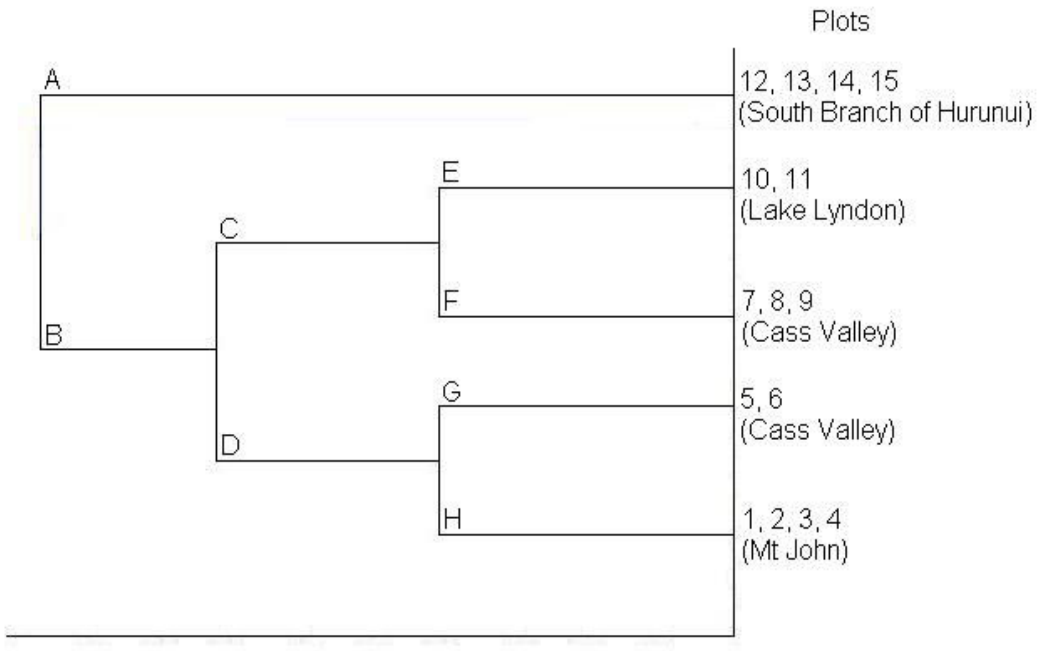

Figure 7 Dendrogram of divisions of plots based on TWINSPAN vegetation compositional analysis (not drawn to scale). Indicator species of each division; A) *Leptinella* sp. C) *Cerastium fontanum* F) *Acenea inermis* G) *Ophiglossum coriaceum*.

H. pilosella covers were highest in plots 3 and 4 (Mt John) with estimated cover greater than 66% of the plot. *H. pilosella* also formed a dominant part of plots 1, 2, 5 and 6 (Mt John and Cass Valley), with 34%-66% estimated cover. It was only a moderate component in plots 7, 8 and 11 (Cass Valley and Lyndon Road) with 1-10% estimated cover, and 11-33% estimated cover in plot 9 (Cass Valley). With less than 1% estimated cover, *H. pilosella* was a minor component of plots 10, 12, 13 and 14, and was absent from plot 15 (Lyndon Road and South Branch of Hurunui). It should also be noted that there was a trend that plots had either high levels of *H. pilosella* or *A. capillaris*; but not both. This is probably due to the differences in the synecology of these two species (Figure 8).

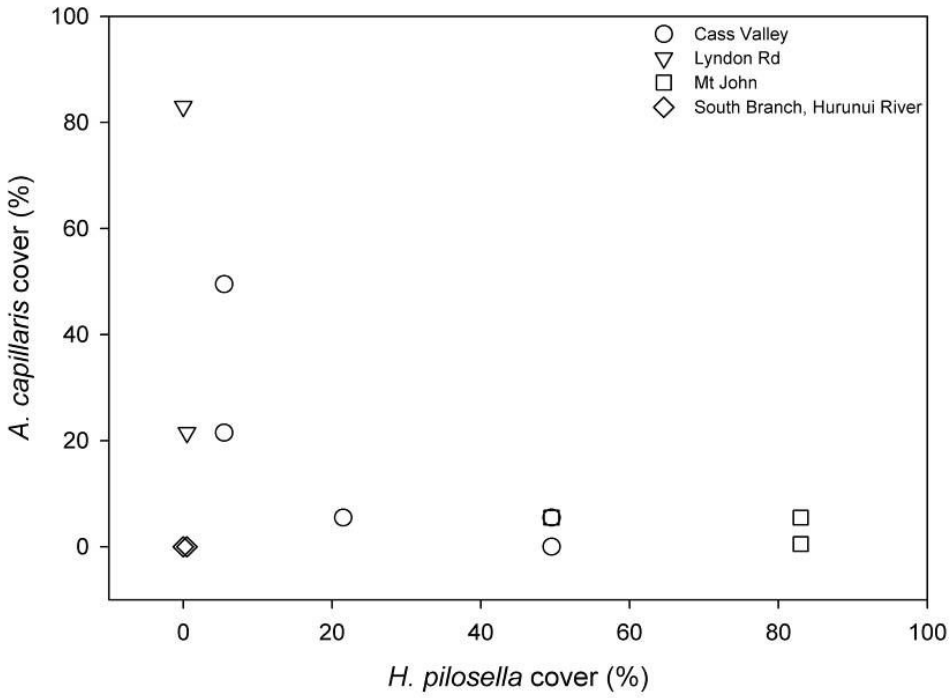

Figure 8 Levels of *A. capillaris* and *H. pilosella* cover in each plot.

Comparing both the overall short tussock (*P. colensoi* and *F. novae-zelandiae*) and *F. novae-zelandiae* density (per hectare) to the amount of *H. pilosella* ground cover (% class midpoint) using Spearman's rank correlation coefficient found that there was a significant correlation (ρ = 0.584 and 0.525 respectively), equating to *P*-values less than 0.05 (Zar, 1972) (Figure 9). *A. capillaris* may also play a role in the density of tussocks because the combined cover of *A. capillaris* and *H. pilosella* is also correlated to the density of both *F. novae-zelandiae* and all short tussocks (ρ = 0.575 and 0.530 respectively, equivalent to $P < 0.05$ (Zar, 1972)). There were also moderate, non-significant correlations between the overall short tussock and *F. novae-zelandiae* basal area (per hectare), and the mean overall short tussock and *F. novae-zelandiae* height (cm), to the amount of *H. pilosella* ground cover (% class midpoint) (ρ = 0.427, 0.364, 0.420 and 0.389 respectively, all equivalent to $0.1 < P < 0.2$(Zar, 1972)). Similar comparisons between basal area of overall short tussock and *F. novae-zelandiae* the combined cover of *A. capillaris* and *H. pilosella*

also give moderate but non-significant correlations (in both cases $\rho = 0.486$, equivalent to $P<0.1$). Significant correlations were detected between both all short tussocks and *F. novae-zelandiae* height, and the combined cover of *A. capillaris* and *H. pilosella* ($\rho =0.545$ and 0.563 respectively, equivalent to $P<0.05$(Zar, 1972)).

Tussock size class distributions (Figure 10) show that generally all the plots have a reverse-J curve ($y=ax^{-3/2}$) with many more small tussocks than large ones; however, in plots 1, 2 10, and 11 *F. novae-zelandiae* clearly has missing size classes below 100 cm^2 tussock basal area with much lower R^2 values of 0.36, 0.21, 0.22 and 0.55 respectively compared to R^2 values for the other plots which range between 0.81 and 0.98

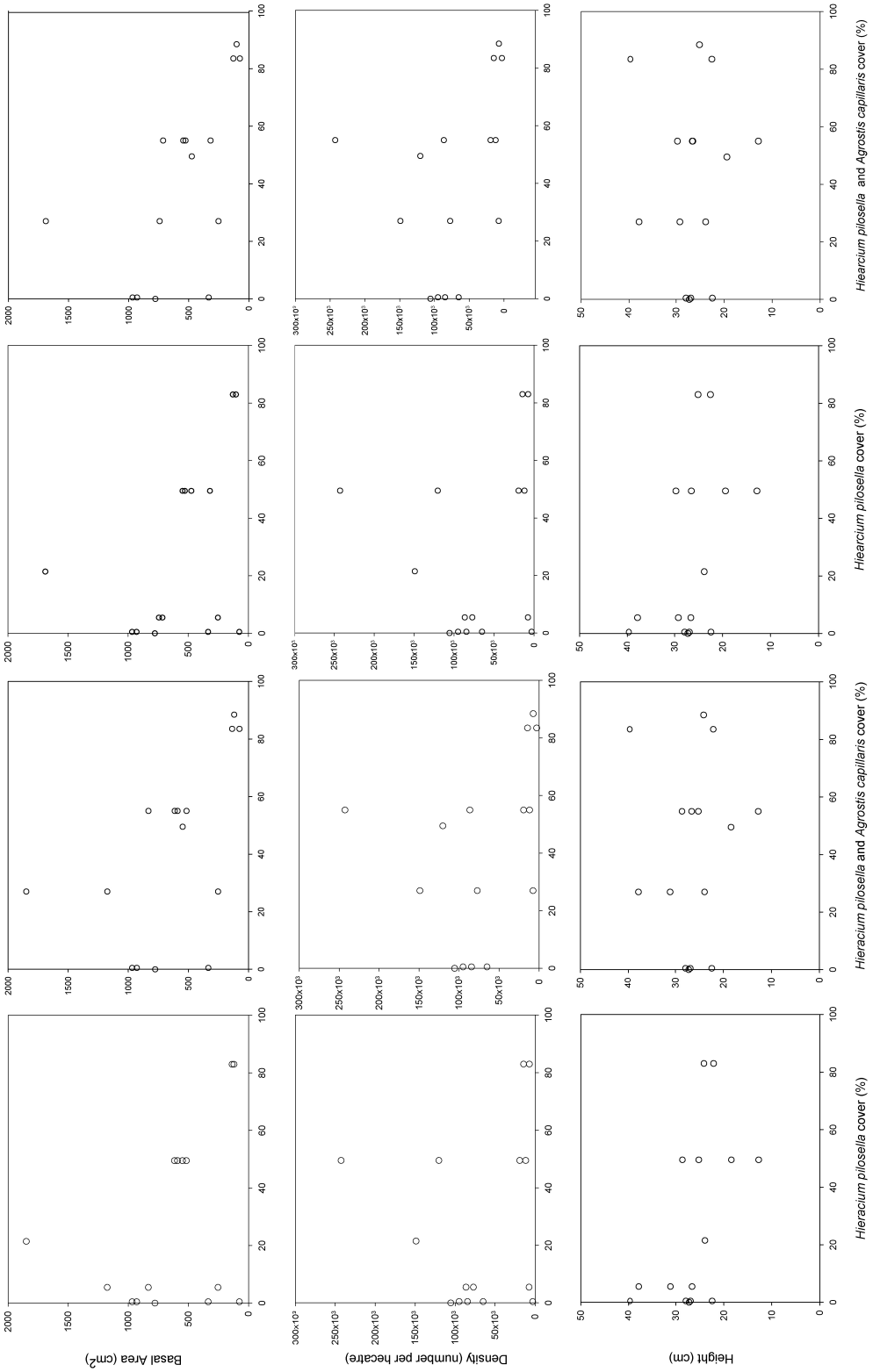

Figure 9 Scatter graphs of mean tussock height, density and basal area against *H. pilosella* cover (% class midpoint).

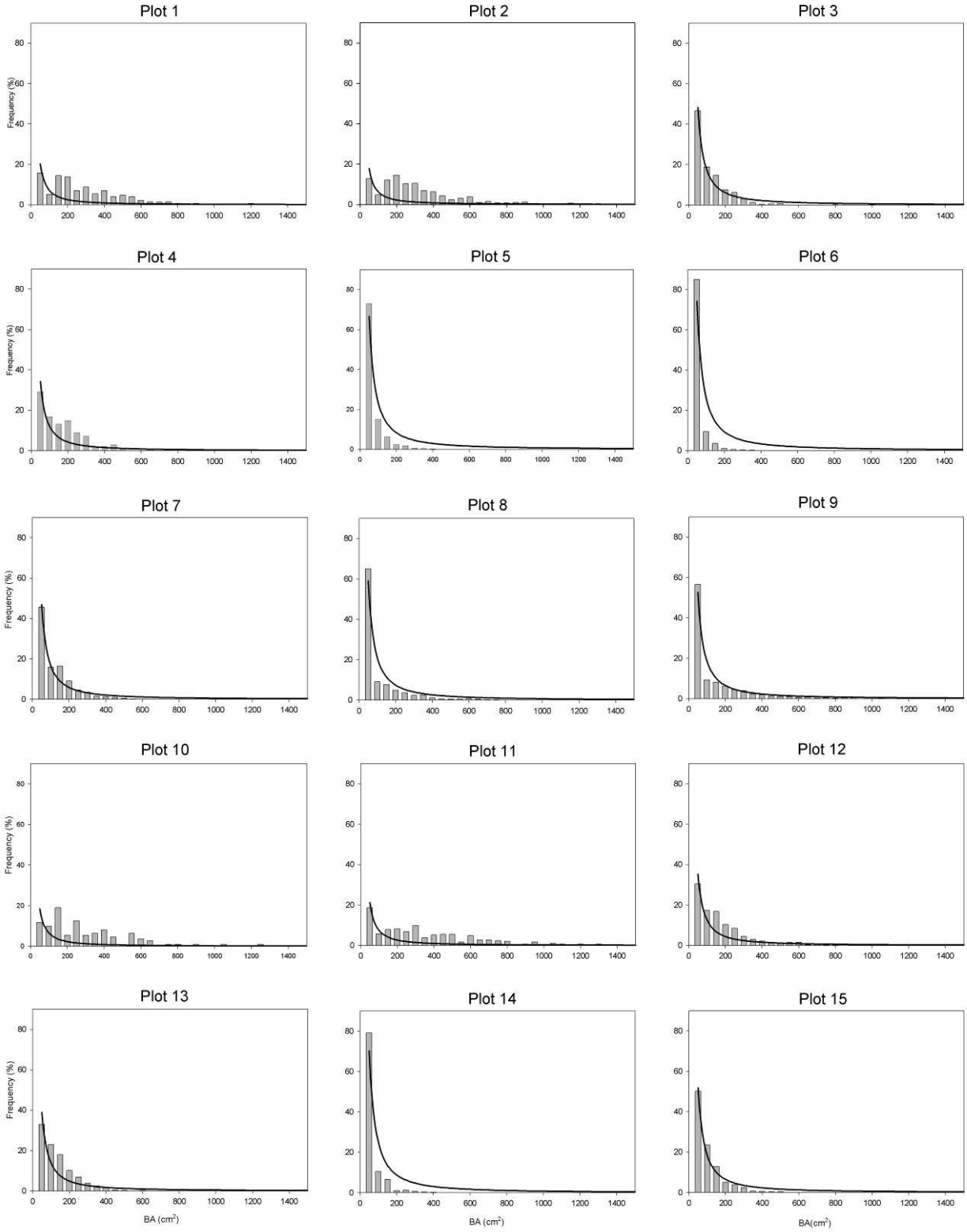

Figure 10 Size class frequency distributions of *F. novae-zelandiae* in each plot, with a fitted reverse J-curve.

The analysis of both *F. novae-zelandiae*'s and all short tussocks' spatial patterns (Appendix 3, and Figure 11 and Figure 12) shows that there are generally two types of spatial patterns (Figure 13). It is important to note that as *F. novae-zelandiae* dominates these tussock grasslands, the patterns of all short tussocks is very similar to those of the *F. novae-zelandiae* tussocks alone. The first type of pattern (plots above the line in Figure 13), typified by plot 12, has regularity or randomness at small scales, followed by a scale of clumping, and randomness at larger scales. The other type of pattern (plots below the line in Figure 13) shows clumping at most scales with regularity or randomness only at small scales; and is typified by plot 4. A Wilcoxon rank sum test comparing the midpoint %cover of *H. pilosella* between these two types of pattern gives a *P*-value of 0.03 which is significant, with the second pattern having a greater mean *H. pilosella* cover (34.5% *cf.* 10.2%).

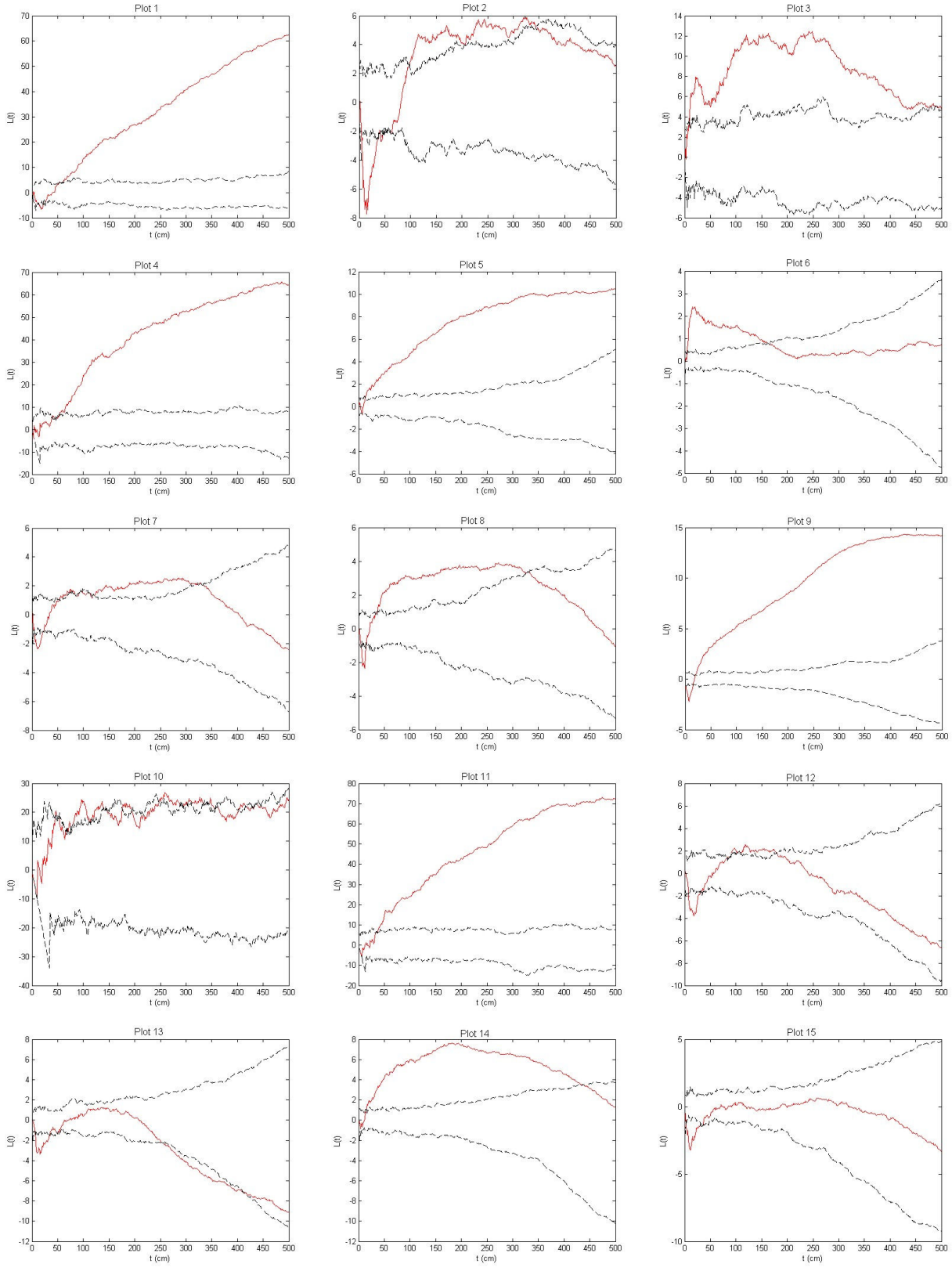

Figure 11 ***Festuca novae-zelandiae*** **Ripley's K-function with Goreaud's transform (*L(t)* = $\sqrt{K(t)/\pi}$-*t*) against the scale of the pattern *(t)*. Solid red line, measured *L(t)*; broken black lines, upper envelope and lower envelopes at α=0.02.**

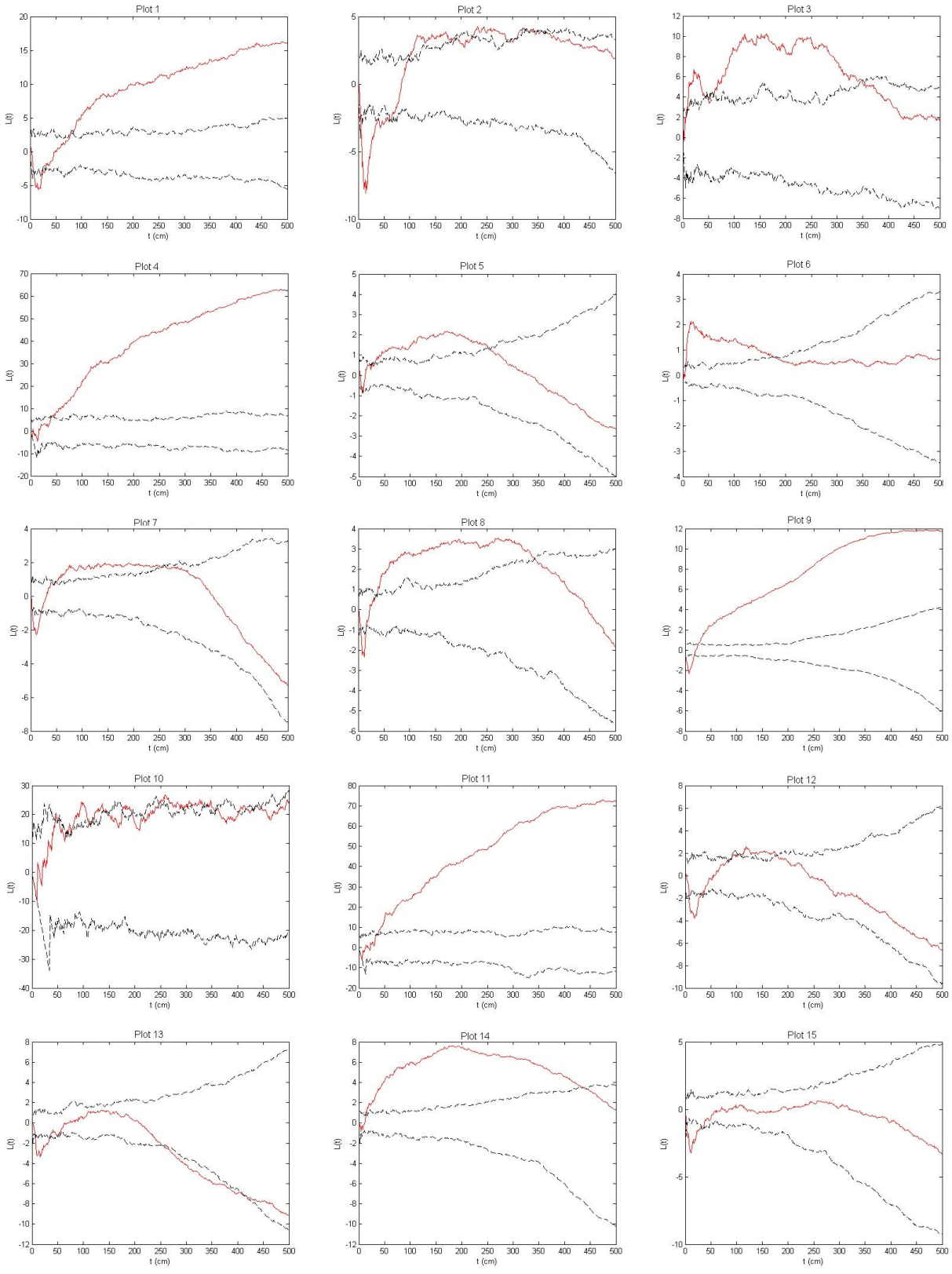

Figure 12 All short tussock species Ripley's K-function with Goreaud's transform ($L(t) = \sqrt{K(t)/\pi} - t$) against the scale of the pattern (t). Solid red line, measured $L(t)$; broken black lines, upper envelope and lower envelopes at α=0.02

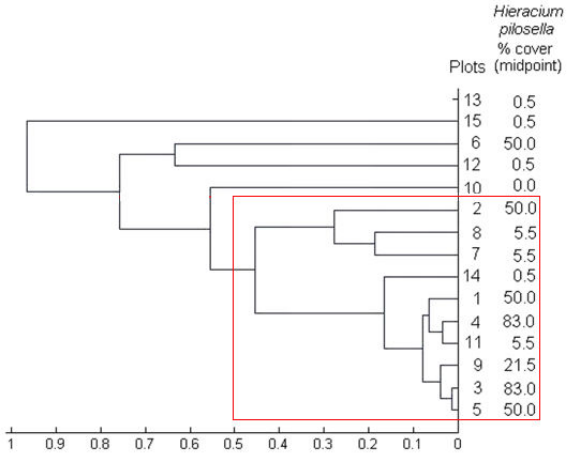

Figure 13 Dendrogram of *F. novae-zelandiae* tussock pattern similarity, the red box indicates the boundary between the two types of patterns, as determined by examining Ripley's K-function.

Discussion

Demographics of tussock populations, as demonstrated through tussock density, basal area per hectare and tussock height, are complex. It is affected by many site characteristics including the site's environment, management and impact of fauna. In addition to the complexity of demographics, the pre-invasion density and basal area of tussocks at each site was probably variable, and it is unknown if the current demographics are different from the pre-invasion levels. However, trends of decreasing density and basal area with increases in *H. pilosella* have been detected (although the later are statistically non-significant), demonstrating a decline in tussocks as the invasion continues which is supported by previous work (Espie, 2001; Johnstone *et al.*, 1999; Scott *et al.*, 1990a, b). The size class frequency distributions of *F. novae-zelandiae* indicates that while a reverse-J model of size classes is generally a good fit for the demographics of tussocks, some plots (1, 2, 10 and 11) have 'missing' size classes below 50cm tussock basal area. This is not related to the level of *H. pilosella,* but may be related to other site characteristics not specifically examined here particularly because both plots at Lyndon Road, and two plots at Mt John have these missing classes. The absence of small size classes indicates that these sites may be suffering from regeneration failure; however, further work looking at regeneration characteristics of this species needs to be carried out before this can be determined. It is interesting to note that the basal

area of tussocks declines more steeply than the density of tussocks which is probably a result of fragmentation of larger tussocks into many smaller ones, maintaining the overall density of tussocks while the basal area decreases (Figure 14). It is hypothesised that the smaller tussocks are more vulnerable to competition than larger ones because they have less resources both above and below ground to exploit; however, the maintenance of the reverse J-curve of size classes despite increasing *H. pilosella* would support the ideas of fragmentation of larger tussocks into smaller ones, as small size classes continue to outnumber large ones across the different invasion levels.

Analyses of the spatial patterns of tussocks in these grasslands indicates that there is increasing aggregation across a range of scales with increases in the ground cover occupied by *H. pilosella* (Figure 14). The increase in aggregation is probably due to *H. pilosella* outcompeting tussocks forcing the tussocks out of marginal microsites. In more favourable refugia microsites the tussocks are more effectively able to compete and retain their position. This proposition is supported by the work undertaken by Moen and Meurk (2001) which showed that *H. pilosella* is generally a stronger competitor than *F. novae-zelandiae;* however, the strength of this competitive effect differs with microsite conditions.

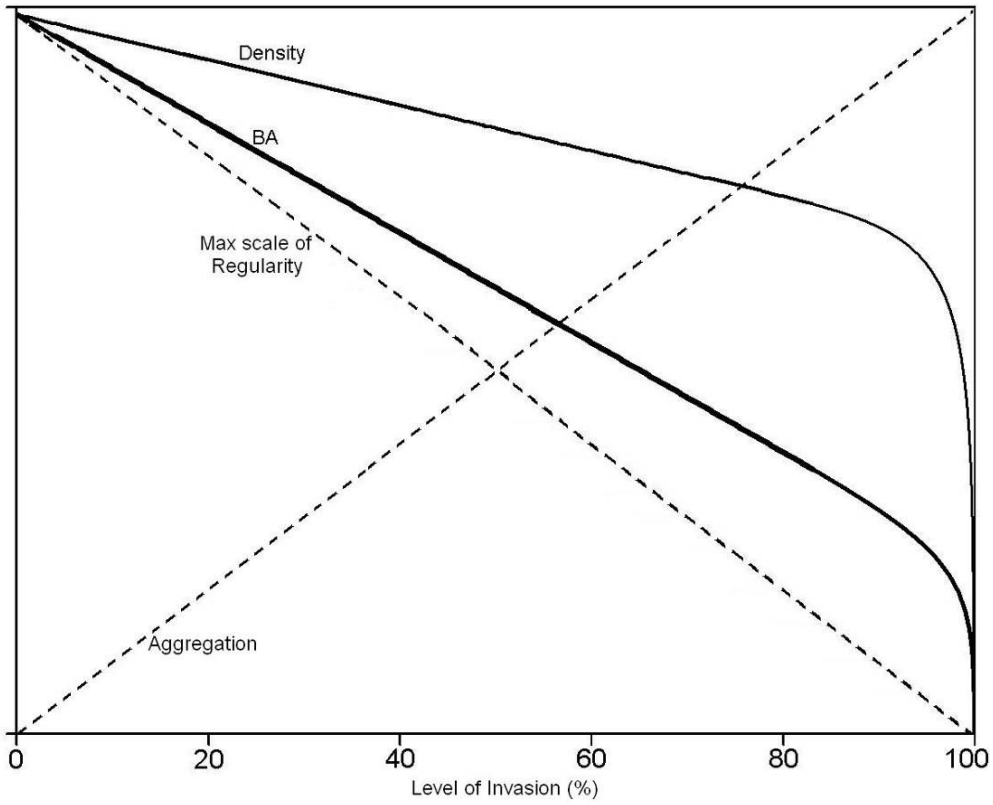

Figure 14 Tussock basal area and density declines, maximum scale of regularity decreases, and aggregation generally increases with increasing levels of invasion.

The observed differences in spatial patterns of *F. novae-zelandiae* also supports the theory that clumping facilitates the co-existence of weaker competitors by increasing intra-specific contact and reducing inter-specific contact, therefore reducing competition between the species (Stoll & Prati, 2001). The clumping of tussocks may also provide shading additional to the overtopping effect of the taller tussocks (Makepeace, 1985a; Moen & Meurk, 2001). Lord's (1992; 1993) investigation of the spatio-genetics of *F. novae-zelandiae* indicates that this clumping is unlikely to reflect familial groups of tussocks, and therefore is not due to vegetative reproduction of tussocks. It is likely that as these clumps of tussocks are further fragmented by *H. pilosella*, the tussocks will become even weaker competitors, escalating the invasion of *H. pilosella*. This increasing invasion of *H. pilosella* after initial establishment has been demonstrated at a wide range of sites in New

Zealand by previous work (Cuff, 1992; Johnstone *et al.*, 1999; Meurk *et al.*, 2002; Scott, 1992; Scott *et al.*, 1990a).

As tussocks are wind pollinated, this fragmentation is probably inconsequential to their reproduction and would be unlikely to cause an allee effect; although, Davis *et al.* (2004) have found some allee effects as a result of pollen limitation on the stand edge of a wind pollinated invasive weed. Scott's (1959; 1961) findings that tussocks dictate patterns of inter-tussock species implies that there are likely to be flow on effects from the fragmentation of tussocks by *H. pilosella* invasion for these weaker competitors which should be further investigated.

In the introduction of this chapter, it was hypothesised that: 1) *F. novae-zelandiae* will have a unique spatial pattern of aggregation and regularity across a range of spatial scales which is common to this species at similar sites, and 2) that this unique spatial pattern will be altered by the invasion of *H. pilosella*. The results discussed above indicate that we should accept these hypotheses that *F. novae-zelandiae* does have a unique spatial pattern of aggregation and regularity across a range of spatial scales which is common to this species at similar sites, and that this pattern is being altered by the invasion of *H. pilosella.*

Chapter 4

The root systems of selected New Zealand short tussock grassland species: description and functional classification

Summary

Belowground competition is thought to be a key interaction shaping grassland plant communities but is generally poorly understood in semi-natural ecosystems. As root system architecture and morphology influences plant resource acquisition, these can be useful for predicting belowground competition intensity between neighbouring plant species. Based on the root systems of 35 New Zealand short tussock grasslands species, we evaluate three published root morphological classification systems and propose a revised functional root classification for the vascular plants of New Zealand's tussock grasslands involving six classes; 1) fibrous roots, 2) long dominant tap root, 3) short tap root with dominant deep laterals, 4) rhizomatous or stoloniferous roots, 5) weakly rooted and 6) short tap root with shallow laterals. By applying this classification to Mackenzie Basin tussock grasslands, we show that plants with short tap roots and shallow laterals are significantly more abundant in modified vegetation at lower altitudes, in contrast to plants that have a long dominant tap root or a tap root with dominant deep laterals which are significantly more abundant in unmodified vegetation at higher altitudes. Rhizomatous or stoloniferous rooted plants do not demonstrate strong trends across environmental or management gradients, showing highly variable abundance.

Introduction

The hidden halves of plants, roots, have many vital functions including anchorage, water absorption and nutrient assimilation. Below-ground competition of roots commonly affects plant production more than above-ground competition, and may be the strongest component of competition in dry or lightly vegetated environments (Casper & Jackson, 1997). In the evolution of rooting strategies there are trade-offs between being able to capture moisture and immobile nutrients, efficiently transport these resources to other organs, and the growth of roots at the

expense of photosynthetic organs (Fitter, 1987). Through the examination of a plant's root system we can make inferences about their below ground functioning and interactions (McIndoe, 1932; Schubert, 1991; Weaver, 1919); however, the morphology of root systems has historically received little attention despite its importance in plant ecology (Wardle, 1991). The specific rooting strategy of species is largely controlled genetically; however, the rooting depth, lateral extent and branching are influenced by environmental conditions such as water availability, temperature, nutrition, and physical and chemical soil conditions, both above and below ground (Doussan *et al.*, 2003; Schubert, 1991; Weaver, 1919, 1920, 1968). The rooting strategy may also change with maturity, though the juvenile stage usually dictates the structure of later roots. The simplification of the range of rooting strategies into similar groups and classifying species by these groups can allow ecological studies to examine trends in below ground relationships and identify species which are vulnerable to competition.

There have been three broad approaches taken towards classifying root systems; morphological, topological and functional. Initial work focused on simple morphology such as the classifications presented by Rimbach, Busgen and Frendenfeldt (Cannon, 1911) who divided the roots of all plants into two groups; 1) intensive or xerophytes with fine terminal roots, highly developed branching and occupation of a small volume of soil; and 2) extensive or hydrophytes with coarse ultimate roots, poor branch development and occupation of a large volume of soil. Cannon (1911) proposed an alternative dichotomy based on studies of desert plant communities, distinguishing between specialized and generalised root systems. This initial classification was later expanded to contain ten different root types based on the presence of primary and adventitious roots, the root branching patterns and position of first order laterals (Cannon, 1949). More recently, Lichtenegger and Kutschera-Mitter (1991) described 13 root types related to the three dimensional shape of the soil volume occupied by the roots. However, their system would not be appropriate for classifying an entire species as this three dimensional shape is dependant on microsite conditions and therefore is highly variable. The only root system classification that has been proposed for New Zealand

was developed by Halloy (1990) as part of a more general morphological classification of New Zealand alpine flora. Five categories of root morphologies were included; tap-rooted, fibrous, radial, parallel and rhizodomorph. All of these simple morphological classification systems do not attempt to reconcile morphology with the functional significance and implications of various traits, and therefore are not useful for predicting plant relationships in ecosystems.

Since the mid 1980s there has been a shift to the use of topological measurements, based on the difficulties in defining clear-cut boundaries between classification groups and the apparent phenotypic plasticity of root systems (Fitter, 1985, 1987). However, topological measurements require full excavation of the root system and many detailed measurements which are time consuming, expensive and can be difficult to make in complex natural and semi-natural systems. Furthermore, topological studies of root systems have been largely focussed on economically important species in amenable soil conditions, resulting in complex models of root growth, but are less suitable for studying root systems in non-cultivated plant communities.

Functional classifications of whole plants have been widely utilised (Gitay & Noble, 1997; Lavorel *et al.*, 1997; Westoby & Leishman, 1997), and some include one or two root traits as part of the classification (Adler *et al.*, 2004; Leishman & Westoby, 1992; Westoby & Wright, 2006); however, few classifications focussed specifically on below-ground functional traits have been proposed due to a lack of detailed knowledge regarding the below-ground functioning of a wide range of plant species. Generally, where data is lacking on difficult to measure functional traits, easily measured "soft traits" are used, such as functionally relevant morphology (Diaz *et al.*, 1992; Díaz *et al.*, 2004; Duckworth *et al.*, 2000; Shugart, 1997; Weiher *et al.*, 1999). However, these soft traits must be used with caution as the relationship between hard and soft traits is not always clear (Violle *et al.*, 2007; Walker & Langridge, 2002) and form does not necessarily correlate directly with specific functions (Lavorel *et al.*, 1997). Weaver (1958a) presented a 'natural' classification based on morphological traits of roots with functional relevance for North American

grassland forbs, and applied this classification to 80 species. The central characteristics of this classification were the depth of rooting and abundance of lateral roots in relation to water availability and interspecific competition.

The short tussock grasslands of New Zealand's eastern South Island are sub-humid and extension of overseas research (Casper & Jackson, 1997) to this environment implicates competition for below ground resources as likely to be more limiting than above ground competition, particularly for water and water soluble nutrients. As such the below ground relationships of plants within grasslands are important to understand the interactions of constituent species. In the absence of detailed field and experimental data on the below ground function of many species present in New Zealand's short tussock grasslands, we evaluate the application of the morphological classification systems proposed by Cannon (1949), Weaver (1958a) and Halloy (1990) to these species, and propose an amended classification system for vascular plants based on general morphology as a soft functional trait. This system is likely to be more widely applicable to New Zealand grassland plants and useful in examining their below-ground relationships.

Methods

Plants were collected from two sites in the Mackenzie Basin, eastern South Island. The Mt John (43° 59' S, 170° 27' E, 760 m) site, west of Lake Tekapo, is part of an AgResearch experimental trial established in 1982 examining various aspects of grazing, fertilizer, irrigation and over-sowing on a *H. pilosella* (hawkweed) invaded *F. novae-zelandiae* (hard tussock) short tussock grassland (Scott, 1999). The site is located on a gently rolling moraine and has a sub-humid climate, receiving *ca.* 600 mm mean annual rainfall and having a mean annual temperature of 8.7°C (Scott, 1999). The Cass Valley site (43° 41' S, 170° 23' E, 1080 m) is located on alluvial flats at the confluence of Alisa Stream and Cass River. The vegetation is again *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland but with localised *Agrostis capillaris* (browntop) on damper soils. Mean annual rainfall is *ca.* 2000mm (New Zealand Meteorological Service, 1985).

A sample of healthy mature plants of all species encountered in six 10.24m^2 plots was excavated for examination of root systems. A total of 35 species were encountered and assessed (Table 3). A sod of soil surrounding the target plant was removed to a depth of *ca.* 30cm using a spade. This depth was found to be sufficient to include the majority of the roots present in the species studied. The diameter of the sod was approximately proportional to the size of the specimen. The soil and neighbouring plants were then carefully removed by either dry brushing or hand washing the sod until only the desired plant remained, attempting to keep as much of the root system as possible intact. These plants were then pressed and mounted as a herbarium vouchers, and lodged at the University of Canterbury's Herbarium (CANU). Existing CANU and Allan Herbarium (CHR) vouchers were also consulted to examine their root systems, however few vouchers included roots. The roots of each of the 35 species examined were described using the classification system proposed here, and the systems of Cannon (1949), Weaver (1958) and Halloy (1990) (Table 3).

Table 2 Summary table of existing root classification systems.

Classification System	Type or Group	Description
Cannon(1949)	Type I	A relatively long primary root system with well developed branching, and with the oldest and longest lateral roots near the soil surface. The roots may occupy a large volume of soil.
	Type II	A relatively short primary root, with first order laterals dominating the upper substratum of the soil.
	Type III	Usually long primary root system, with many short first order lateral shoots.
	Type IV	Long and slender primary root, with well branched first order laterals. Those closest to the surface are longest.
	Type V	A primary root system which is divided with few or no first order lateral roots.
	Type VI	A primary root system which is divided with almost all of the first order laterals occurring in the upper substratum of the soil.
	Type VII	An adventive centralized uniformal root system.
	Type VIII	An adventive centralized multiformal root system.
	Type IX	An adventive decentralized uniformal root system.
	Type X	An adventive decentralized multiformal root system.
Weaver (1958)	Group I	Characterised by a taproot with branches which arise in the first three feet of soil and spread widely and deeply, thereby absorbing water from deep in the soil, below the reach of the grasses.
	Group II	With their abundant laterals in the surface 1 to 2 feet, these species directly compete with grasses in dry soils which can be very compact. Development in response to dry soils with only light precipitation in summer.
	Group III	The taproots have few branches but penetrate deeply, and probably absorb water throughout their range.
	Group IV	Characterised by having rhizomes, root offshoots or corms with numerous roots and indefinite lateral spread, and are vigorous competitors of grasses by strongly absorbing water at the soil surface.
Halloy (1990)	Tap	Generally strongly tapered with only a few per plant and slight branching.
	Radial	Roots radiating from a concentrated origin with few branches.
	Fibrous	Usually wiry and typically densely branched.
	Parallel	Decentralized root system which is longer than 10mm.
	Rhizodomorph	Decentralized root system which is shorter than 10mm.

Table 3 The application of Cannon (1949), Weaver (1958), Halloy (1990) and the proposed root system classification to species of New Zealand's short tussock grasslands.

Species	Canon (1949)	Weaver (1958)[4]	Halloy (1990)	Proposed Classification
Acaena inermis	IX	IV	Parallel	Rhizomatous or stoloniferous
Agrostis capillaris	VII	n/a	Fibrous	Fibrous
Anisotome aromatica	V	II	Tap	Long dominant tap root
Anthoxanthum odoratum	VII	n/a	Fibrous	Fibrous
Brachyglottis bellidioides	[5]	III	Radial	Tap root with deep laterals
Carmichaelia vexillata	I	I	Tap	Long dominant tap root
Celmisia gracilenta	VII	II	Radial	Short tap root with shallow laterals
Cerastium fontanum	VI	II	Tap	Short tap root with shallow laterals
Chionochloa rubra	VII	n/a	Fibrous	Fibrous
Coprosma perpusilla	IX	IV	Parallel	Rhizomatous or Stoloniferous
Craspedia lanata	VII	I	Radial	Short tap root with dominant deep laterals
Festuca novae-zelandiae	VII	n/a	Fibrous	Fibrous
Geranium sessiliflorum	VI	II	Tap	Long dominant tap root
Hieracium pilosella	II	II	Radial	Short tap root with shallow laterals
Hieracium praealtum	II	II	Radial	Short tap root with shallow laterals
Leucopogon fraseri	X	IV	Parallel	Rhizomatous or stoloniferous
Linum catharticum	I	I	Tap	Weakly rooted
Luzula rufa	VII	n/a	Fibrous	Fibrous
Microtis oligantha	VIII	IV	Radial	Weakly rooted
Ophioglossum coriaceum	II	II	Radial	Weakly rooted
Pimelea oreophila	IV	II	Tap	Long dominant tap root

[4] Weaver (1958) does not apply to graminoid species.

[5] This species does not fall into any type given by the classification

Poa colensoi	VII	n/a	Fibrous	Fibrous
Poa maniototo	VII	n/a	Fibrous	Fibrous
Poa novae-zelandiae	VII	n/a	Fibrous	Fibrous
Prasophyllum colensoi	VIII	IV	Radial	Weakly rooted
Pyrrhanthera exigua	IX	IV	Parallel	Rhizomatous or stoloniferous
Raoulia australis	IX	IV	Fibrous	Fibrous
Raoulia hookeri	IX	IV	Fibrous	Fibrous
Raoulia parkii	IX	IV	Fibrous	Fibrous
Raoulia subsericea	IX	IV	Fibrous	Fibrous
Rumex acetosella	IX	IV	Parallel	Rhizomatous or stoloniferous
Trifolium arvense	I	II	Tap	Weakly rooted
Trifolium repens	VI	II	Tap	Rhizomatous or stoloniferous
Veronica avensis	IV	II	Tap	Weakly rooted
Wahlenbergia albomarginata	IX	IV	Fibrous	Rhizomatous or stoloniferous

We then applied our proposed root classification to a vegetation data set collected from Glenmore Station, Lake Tekapo, which includes the Cass Valley site and lies just north of the Mt John site. As part of a broader land cover monitoring programme across high country farms (Norton *et al.*, 2006), 52 permanent land cover monitoring sites were located on Glenmore Station to be broadly representative of the main vegetation types present. Cover abundance data for vascular plants (visually assessed using cover classes of <1, 1-5, 6-10, 11-25, 26-50, 51-75 and 76-100% in a 16 m^2 area at each monitoring site) were then classified using the polythetic divisive technique of indicator species analysis (Hill *et al.*, 1975) as implemented in TWINSPAN (Hill & Šmilauer, 2005). After examining the divisions, the second level was used for classification yielding four groups. These four vegetation types were then used as the basis for assessing the utility of our root classification system for distinguishing between different vegetation types within tussock grassland vegetation. Comparisons of the abundance of different root types in these vegetation groups were

undertaken using single-factor analysis of variance (ANOVA) with arcsine transformations to the cover abundance data and a comparisonwise error rate of 0.001. Where significant differences were detected, this was followed by multiple comparison t-tests with Bonferroni's correction to determine where the differences occur (experimentalwise error rate of 0.05).

Evaluation of existing root classification systems

Cannon's (1949) root morphology classification system has ten types (Table 2), with types I to V related to primary root systems and types VI to X related to adventive root systems. This system of classification encompasses much of the variation expressed in the root systems of New Zealand's short tussock grassland species, with only one species unable to be classified, *Brachyglottis bellidioides* (Table 3). However, this classification does not focus on functional aspects of root morphology and the ecological implications of the various types are not fully explored by Cannon (1949).

Unlike Cannon's (1949) classification system, Weaver's (1958) system incorporates functional aspects of root morphology, particularly regarding competition and water absorption. It comprises four groups (Table 2) and is based on the extensive excavation and examination of the forbs of North America's prairies. However, this classification addresses only forbs, and does not represent the full range of root systems examined by Weaver (1958), with grasses, many woody plants and even one forb in Weaver's data not able to be classified by his system. It is therefore not possible to apply this system to the full range of plants found in New Zealand short-tussock grasslands.

Halloy's (1990) system of morphological classification is simple and easy to apply with only four root systems represented; tap, radial and parallel roots and rhizodomorph (Table 2). Halloy (1990) also suggested using plurimere (6-50 apices), paucimere (2-5 apices), solitary (one apex), woody, graminoid, tenuous, tuberous, spongy or fleshy as further descriptors. These descriptors have not been used in the present study as they are thought to be closely correlated to the basic groupings, adding little to the classification system. The simplicity of Halloy's (1990) classification means

that variation with important ecological implications is lost, such as the differentiation between root systems which are dominantly shallow compared to those which are deep. Also, like Cannon (1949), the functional facets of root morphology have not been explored in this classification, and as such ecological implications of the root system types are unclear.

Although each of the above systems could be applied to New Zealand's short tussock grasslands (Table 3), the inherent problems discussed above limit their efficacy. The classification system proposed below enhances the advantageous aspects of these systems while addressing these limitations, to provide a system which is tailored for and works well in New Zealand's short tussock grasslands.

The proposed root classification system

The classification of seven root morphologies presented here (Figure 15) attempts to be simple but expands Halloy's (1990) and Cannon's (1949) root morphologies to consider characteristics which are thought to be important for the functioning of roots, including root surface area, branching, rooting depth and the opportunity cost of growth, thus building in some of the functional attributes considered by Weaver (1958).

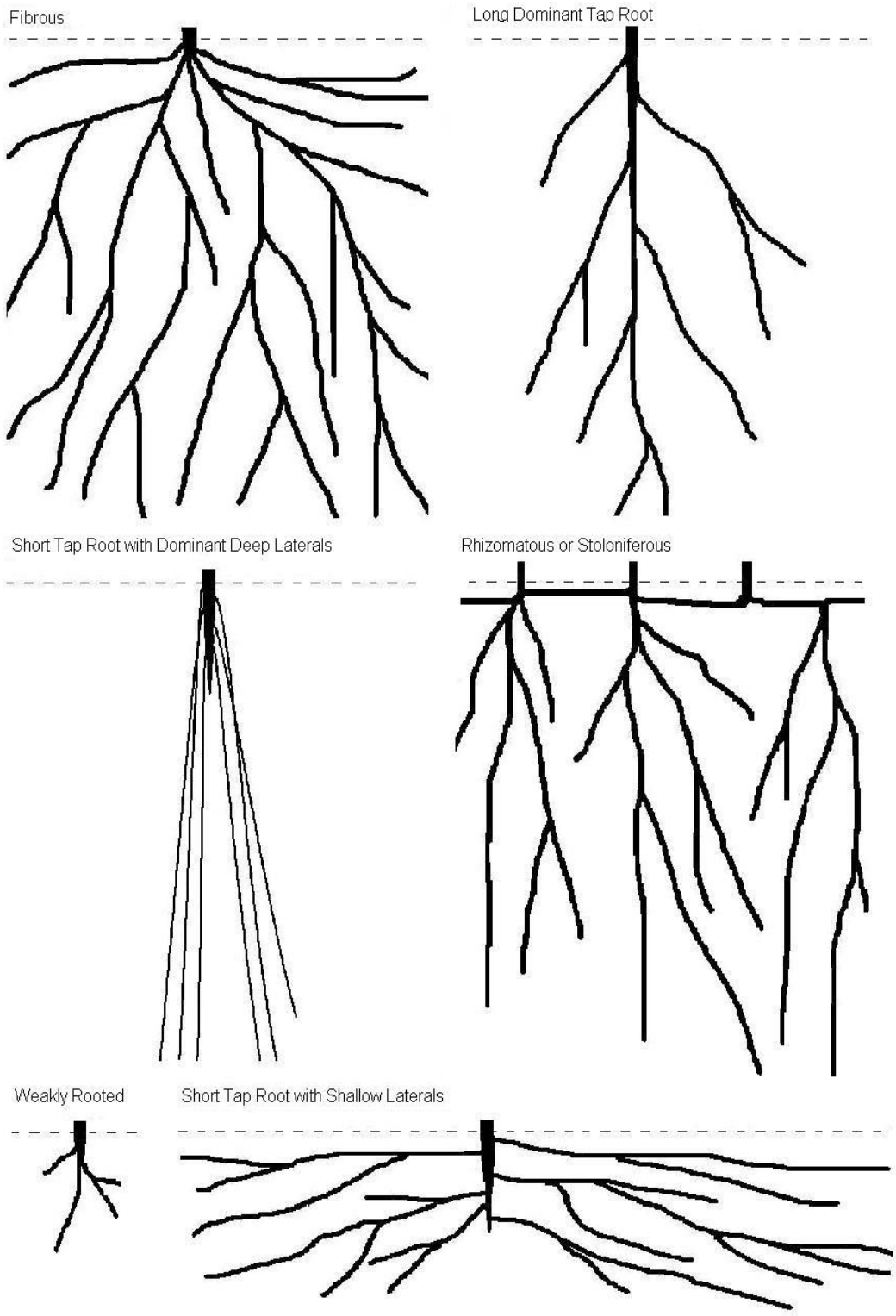

Figure 15 Pictorial profile diagrams of root functional groups

Fibrous roots

This group of species is equivalent to Halloy's (1990) fibrous root and Cannon's (1949) type VII, with many adventitious roots arising from one area and typically dense branching. Generally, mature monocotyledonous species have this type of root system as their anatomic structure prevents secondary thickening of roots. Without secondary thickening, monocotyledons are restricted to increasing the length and number of roots in order to increase the root surface area which is important for nutrient and water absorption (Casper & Jackson, 1997). These plants are usually strong competitors for immobile nutrients and water, especially in relatively dry conditions (when water soluble nutrients become relatively immobile), as they occupy a large volume of soil with many small roots (Casper & Jackson, 1997), on the other hand, the large root network is not considered very efficient at transporting nutrients to the shoots of the plant (Fitter, 1987).

Typical species: *Festuca novae-zelandiae* (Hack.)Cockayne (CANU 25359, 38964, 38965, 8966, CHR 580699), *Agrostis capillaris* L. (CANU38943, 38944, 38945)

Long dominant tap root

With a long dominant tap root and well developed branching, these plants may occupy a large volume of soil. The tap root itself is thick and deep and may have many or few lateral branches and fine roots. This description is closest to type V of Cannon (1949), groups II and III of Weaver (1958) and tap root of Halloy (1990). This type of root system is able to exploit deeper resources in the soil thereby avoiding competition with shallower root systems through the division of resources spatially (Casper & Jackson 1997).

Typical Species: *Pimelea oreophila* C.J.Burrows (CANU 38984), *Carmichaelia vexillata* Heenan. (CANU 38954, CHR 217862)

Short tap root with dominant deep laterals

With either a long or short tap root, the lateral roots in these plants are long and thick, dominating the architecture of the root system. This type of root system is dissimilar from those described in

Cannon (1949), not matching any of his root descriptions; but may be included in group III of Weaver (1958) and either the tap or radial classifications in Halloy (1990), depending on the size of the tap root. Similar to dominantly tap rooted species, these plants are able to avoid competition with shallow rooted species by dividing resources spatially (Casper & Jackson 1997); however, by having multiple long roots these plants are also given greater opportunities to tap into dispersed localised pockets of resources compared to dominantly tap rooted species (Casper & Jackson 1997).

Typical Species: *Brachyglottis bellidioides* (Hook.f.) B.Nord. (CANU 38950, 38951, 38952, 38953, CHR 197046, 58657), *Craspedia lanata* (Hook.f.)Allan (CANU 38961)

Rhizomatous or Stoloniferous

This group corresponds to Halloy's (1990) parallel root system, but has been expanded to include those species which have rooting along a prostrate stem which is not necessarily vertically parallel and may be heavily branched. These root systems are dominated by the presence of horizontal stems either above or near the soil surface (rhizome or stolon), which root along their entire length. These roots can be fine and fibrous or develop into parallel vertical primary roots. These species are also strong competitors for immobile nutrients or in relatively dry conditions due to the large surface area (Casper & Jackson 1997); however, the transportation of nutrients from the roots to shoot of a plant is likely to be more efficient due to the shorter distance between them (Fitter 1987). The horizontal stems also allow the plant to spread more widely, providing greater opportunities to tap into localised pockets of resources (Casper & Jackson 1997).

Typical species: *Pyrrhanthera exigua* (Kirk)Zotov. (CANU 6899, 38990, 38991, CHR 21056, 318021), *Wahlenbergia albomarginata* Hook.f. (CANU 4207, 35536, 39004, 39005)

Weakly rooted

These root systems are composed of generally fine roots with or without a tap root, which do not penetrate deeply or widely into the soil. They are poorly branched, and occupy only a small

volume of soil relative to the size of the above ground shoots of the plant. Roots of this type are not specifically catered for in Cannon (1949), Weaver (1958) or Halloy (1990), and is divided across many of the groups within those systems. These species are generally short lived annuals or have the ability to utilise mycorrihzal association, thereby avoiding the need for extensive root systems (Casper & Jackson 1997). The annual plants are able to avoid competition by dividing resources temporally, utilising resources in times of abundance and avoiding competition during drought (Casper & Jackson 1997).

Typical Species: *Linum catharticum* L. (CANU 38980, CHR 151141, 192008), *Trifolium arvense* L. (CANU 39002, 23955, 3137), *Microtis oligantha* L.B.Moore (CANU 38982, CHR 189032)

Short tap root with shallow laterals

This group of species have tap roots which are generally less than 5cm long, with many longer first order lateral roots which branches in a horizontal direction forming a dense network of roots in the upper soil stratum. This description fits neatly into type II of Cannon (1949) and group II of Weaver (1958); however, it does not clearly belong in any of the groups of Halloy (1990) being most closely aligned his radial or fibrous groups. This has similar advantages as the fibrous tap root, being able to strongly compete for immobile nutrients (Casper & Jackson 1997); however, the addition of secondary thickening of the roots allows for more efficient transportation of absorbed nutrients to the shoots of the plant (Casper & Jackson 1997). Weaver (1958b) proposed that this root system may have advantages where precipitation is light, and is not absorbed deeply into the soil.

Typical Species: *Hieracium pilosella* L. (CANU 38969, 38970, 38971, 38972, 38973, 38974) *Celmisia gracilenta* Hook.f. (CANU 38955, 38956)

Application to Short Tussock Grasslands

Classification of the 35 species present at the Mt John and Cass River study sites (Table 3) shows that 34.3% of these species had fibrous roots, 20% rhizomatous or stoloniferous roots, 17.1%

weakly rooted, 11.4% long dominant tap root, 11.4% short tap root with shallow laterals and only 5.7% had a tap root with deep laterals. However, the proportion of species in each classification does not indicate the real abundances of these root functional groups in grassland ecosystems and it does not take into account the relative abundance of individual species or their biomass.

The TWINSPAN analysis carried out here resulted in four vegetation types that correspond to both land management and environmental gradients identified on Glenmore Station by Norton *et al.* (2006) (Table 4). Both the over sown and degraded short tussock grasslands occur at significantly lower elevations (796 and 865 m) than the tall tussock grassland and degraded tall tussock grassland (1266 and 1309 m). The tall tussock grassland is also situated on significantly steeper sites than any of the other three vegetation types (24° *cf.* 7°, 10°, 12°). The over sown short tussock grassland has had the most intensive management inputs compared to the other vegetation types, and comprises areas which have been aerially over-sown and top-dressed (Norton *et al.*, 2006), while both the degraded short tussock grassland and degraded tall tussock grassland have high ground covers of *Hieracium pilosella*, an invasive weed.

Table 4 Vegetation description, management, elevation and slope of Glenmore Station's four grassland vegetation types.

Vegetation Type	Description[†]	Management	Elevation	Slope
Over sown short tussock grassland	(Hard tussock)-(Browntop)/clover[‡]-(hawkweed) grassland	Aerially over sown, top dressed and grazed	796m ± 49	7.6° ± 6.5
Degraded short tussock grassland	Hawkweek herbfield	Grazing	865m ± 84	10.7° ± 11.2
Degraded tall tussock grassland	(Tall tussock)/hawkweed grassland	Grazing	1266m ± 285 *	12.3° ± 9.4
Tall tussock grassland	(Tall tussock)-(short tussock) grassland	Grazing	1309m ± 148 *	24.2° ± 6.6 *

* Significant difference [†] brackets indicate greater than 20% mean cover [‡] Trifolium arvense and Trifolium repens

Significant differences are apparent in the abundance of the root functional groups among these four vegetation types (Figure 16). Fibrous rooted species are generally a major component of these systems as would be expected in a grassland, however their proportion of cover abundance is significantly lower in degraded short tussock grassland plots than others (11.2% *cf.* 25.7, 37.7 and 39.7%). Species with a short tap root and shallow laterals (e.g. *H. pilosella* and *Celmisia gracilenta*) were significantly more abundant in the degraded short and tall tussock grasslands (46.7 and 39.1%) than in the other types (11.9 and 9.7%). These sites have been moderately modified and this effect is likely due to the high invasion of *H. pilosella*. Dominantly deeply tap rooted species were generally a minor component of these vegetation types but occupy significantly more of the ground cover in tall tussock grassland plots than any of the other vegetation types (19.8% *cf.* 1.9, 2.9 and 4.9%). Tap rooted species with deep laterals were also significantly higher in tall tussock grasslands, being absent from both the over sown and degraded short tussock grasslands and only a minor component of degraded tall tussock grassland. In contrast, the weakly rooted species were significantly higher in over sown short tussock grasslands, moderate in degraded short tussock grasslands and low in both the tall tussock grasslands and degraded tall tussock grasslands. Of the root functional groups examined, Rhizomatous or Stoloniferous species were the only ones not to significantly differ amongst the vegetation types, and do not appear to be significantly affected by the environmental and management gradients identified. The proportion of rhizomatous and stoloniferous species was greatly variable ranging from absent to up to 50% of the plot's vegetative cover.

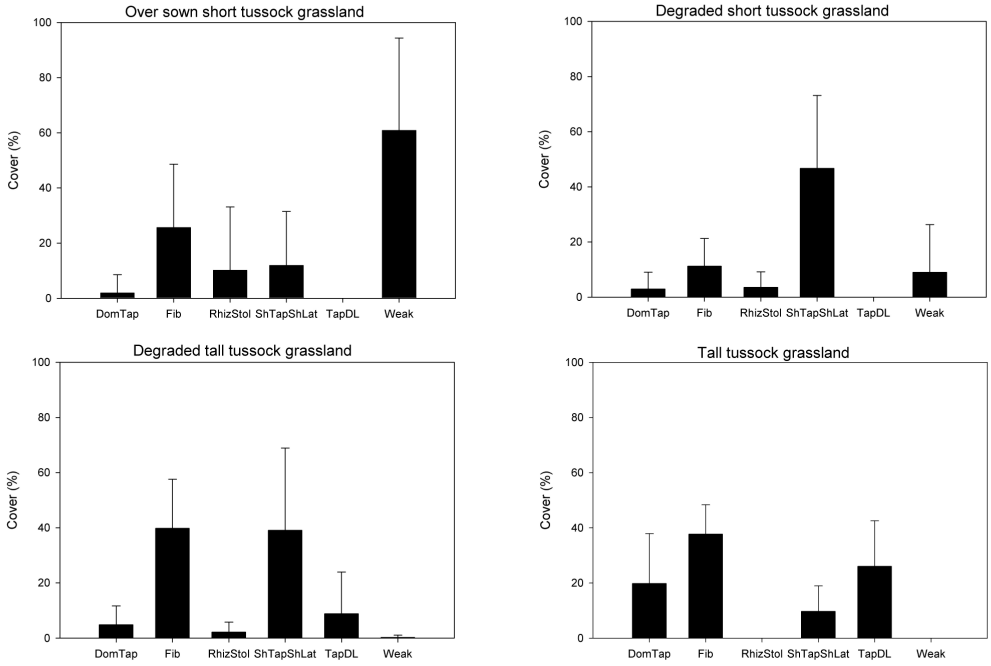

Figure 16 Percentage ground cover of six different root functional groups within Glenmore Station's four vegetation types. DomTap (long dominant tap root), Fib (fibrous), RhizStol (rhizomatous or stoloniferous), ShTapShLat (short tap root with shallow laterals), TapDL (tap root with dominant deep laterals), Weak (weakly rooted). The error bars represent one standard error from the mean.

Generally the root systems of the over sown and degraded short tussock grasslands and the degraded tall tussock grassland are shallow, with short tap shallow laterals and fibrous root systems, forming a dense network of roots in the upper soil layers. The competition between individuals in this dense mat of roots is thought to be high, with only a small proportion of the plants avoiding competition by dividing resources spatially or temporally. The tall tussock grassland has a greater propensity for deep roots. This may be associated with the higher altitudes and heavier rainfalls which infiltrate the substrate further, but also with the lower intensity of land management.

Discussion

Morphological and functional classification facilitates the study of root systems, as it reduces complexity but allow the identification of broad trends. Contrary to Weaver's (1958) observations that there are great variations of root structures even within genera, we have found that species with the same taxa are generally similar, for example both *H. pilosella* and *Hieracium praealtum*

have short tap roots with shallow lateral roots and all four *Raoulia* spp. examined have fibrous root systems. This similary is expected, given that evolutionary theories hypothesize that species from closely related evolutionary lineages will be more similar in their ecological traits than species from very distant lineages (Felsenstein, 1985). However, the two *Trifolium* spp. examined have appreciably different root structures. There are also similarities amongst some higher taxa, for example all the members of Poaceae examined have fibrous root systems.

This classification may also be useful in identifying those species which are most vulnerable to the invasion of weeds (Pokomy *et al.*, 2005) or identify which species most strongly compete for underground resources. Those which share similar root morphologies are likely to utilise similar resources. If this is the case, *H. pilosella*, which is a major invasive weed of New Zealand's short tussock grasslands, would most strongly compete with other exotics *Cerastium fontanum* and co-generic *Hieracium praealtum*, and more importantly the native daisy *Celmisia gracilenta*. As it is a shallowly rooted species, *H. pilosella* is likely to also be a strong competitor with other predominantly shallowly rooted species such as the rhizomatous or stoloniferous, and weakly rooted species.

All classifications based on morphology, whether functionally relevant or not, have similar problems of continuous variation and environmental influences on morphology; however, below ground morphologies have the added problems of excavation. By focusing on the general morphology in the proposed classification as opposed to precise rooting depths, the difficulties associated with excavating the entire root system undamaged are reduced.

The examination of root systems of further species, and comparisons in a range of herbaceous communities would be of benefit to the refinement of this functional classification system and may provide insight into the below ground relationships of these plant communities.

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Chapter 5

Spatial patterns of inter-tussock species in New Zealand's *Hieracium pilosella* invaded short tussock grasslands

Summary

Spatial arrangements of plants reflect and affect ecological processes as plants interact mainly with their direct neighbours (Murrell *et al.*, 2001; Pacala, 1997). *Hieracium pilosella* is an invasive weed of short tussock grasslands in New Zealand (Espie, 2001). Eleven 10.24m^2 plots, with 4096 subplots each, were established across a gradient of *H. pilosella* invasion using four different sites; and analysed using join-count statistics and modified Ripley's K and K_{12}-functions (Fehmi & Bartolome, 2001) to find inter- and intra-specific spatial patterns of scales up to 160 cm. The invasion of *H. pilosella* is correlated with changes in the spatial patterns of plant species, life-forms and root functional groups (structural fragmentation); however, the specific changes differ between groups. This structural fragmentation of the vegetation is likely to have flow on effects for both invertebrates and the reproduction of plant species.

Introduction

The spatial patterns of vegetation in an ecosystem is the result of all current and past ecological processes (Legendre, 1989), and will have implications for future processes as ecology is an inherently spatial science (Dale, 1999; Fortin & Dale, 2005). Also, all plants primarily interact with their direct neighbours (Murrell *et al.*, 2001; Pacala, 1997; Silvertown *et al.*, 1992) and their environment, making the study of small-scale spatial patterns in vegetation an important area of enquiry.

Hieracium pilosella is a widespread invasive weed of the New Zealand's South Island hill and high country, with significant impacts on both agricultural and ecological values (Espie, 2001). *H. pilosella* replaces the native short-tussock grassland vegetation, alters soil properties (Boswell & Espie, 1998; McIntosh & Allen, 1993; Powell *et al.*, 1997; Scott *et al.*, 2001) and at some sites may increase the area of bare ground in these plant communities (Johnstone *et al.*, 1999; *c.f.*

Rose *et al.*, 1995; Rose *et al.*, 2004); while having little grazing value due to its apressed foliage (Espie, 2001).

The invasion of exotic species can have a range of effects on indigenous ecosystems, including fragmentation (Reaser *et al.*, 2007). Fragmentation is the breaking up of continuous habitat into isolated remnants, the scale of which can vary greatly(McIntyre & Hobbs, 1999). The premise of structural fragmentation as proposed by Lord and Norton (1990) is fragmentation which occurs at the smallest scales, isolating individuals within a community. Generally, the size of the organism affected is proportional to the scale of fragmentation (Lord & Norton, 1990); therefore the invasion of the small herb *H. pilosella* may be causing structural fragmentation, affecting even the smallest of organisms in the invaded plant community.

Generally, studies which have addressed competition and spatial arrangement of plants have concluded that spatial patterning is important to competitive interactions between individuals, with intra-specific aggregation reducing competition between species and therefore increasing co-existence (Murrell *et al.*, 2001; Potthoff *et al.*, 2006; Stoll & Prati, 2001). However, de Broeck *et al.* (2006) suggested that aggregation could also lead to vulnerability to invasion through available resources not being utilised by the lack of complementarity.

Scott (1959; 1961) investigated spatial relationships between tussocks and inter-tussock species prior to the invasion of *H. pilosella*, using nearest neighbour methods. He found that the patterns of inter-tussock species were dictated by the position of tussocks, with inter-tussock species forming concentric rings of different radii centred on the tussocks. No work has been undertaken to re-examine these spatial patterns since the invasion of *H. pilosella*. Other non-spatial research has indicated that small inter-tussock herbs, such as *Celmisia gracilenta*, *Wahlenbergia albomarginata, Luzula rufa* and haresfoot trefoil (*Trifolium arvense*), are highly vulnerable to the invasion of *H. pilosella* (Duncan *et al.*, 2001; Willis *et al.*, 1992). It is hypothesized that this vulnerability will be reflected in changes to their spatial patterns.

This chapter focuses on the spatial patterns of New Zealand's short tussock grassland plant species using spatial statistics, and how these spatial patterns have been altered by the invasion of *H. pilosella*. These spatial statistics identify scales of aggregation and regularity both within species and between species. Where aggregated, species are found within a specified scale more often than expected if the pattern was spatially random. Aggregation would be expected where vegetative reproduction is important, seeds do not fall far from the parent, there are strong microsite preferences in a patchy heterogeneous environment, or facilitation between individuals is occurring. Alternatively, regularity is where individuals are found within a specified scale less often than expected if the pattern was spatially random. The presence of regularity is indicative of a competitive or negative effect between species, as the strongest competitor prevents the germination and/or survival of the other species in adjacent areas. Specifically, this chapter seeks to 1) determine if there are consistent spatial patterns in New Zealand's short tussock grasslands at relatively small scales; 2) investigate how the invasion of *H. pilosella* may be altering these spatial patterns; and 3) establish if the spatial patterns of species are being altered in different ways. As plant community composition differs between sites making it difficult to come to conclusions about the patterns of uncommon species across all sites, life form and root functional groups will also be employed. The use of life forms and root functional groups may also allow conclusions about plant spatial patterns to be inferred for other sites with similar plant communities

Study Sites

It was not possible to locate environmentally similar sites with a range of *H. pilosella* invasion levels as generally in Canterbury the only short tussock grassland sites with low or no *H. pilosella* invasion are in cooler locations with relatively high mean annual rainfalls (Walker & Lee, 2000, 2002). As a result the four sites utilised (South Branch of Hurunui River, Lyndon Road, Cass Valley and Mt John) have climates that are disparate to some extent. However, all of the sites are similar in that they are *Festuca novae-zelandiae* short tussock grasslands with grazing of either

domestic stock and/or wild mammalian herbivores, very little or no slope, generally good drainage, low fertility, and no history of fertilisation or over sowing.

South Branch of the Hurunui River is one of the few sites of *F. novae-zelandiae* short tussock grasslands which are not significantly invaded by *H. pilosella*. Its proximity to the main divide of South Island means that it is subject to a strong orographic rainfall effect and has relatively high mean annual rainfall (Table 1). The cool moist climate, relative isolation, and lack of recent farming history has probably protected this area from the invasion of *H. pilosella*; however the presence of *H. pilosella* has increased since Walker and Lee's (2002) survey . The alluvial nature of these grasslands means that the soils can be very thin in some areas. As this area is under the management of the Department of Conservation, it is not actively managed for agricultural grazing; however feral hares do have a visible impact on the flats.

Lyndon Road connects Lake Coleridge to Lake Lyndon in inland mid Canterbury. The study site itself is situated on the eastern side of Lyndon Road, approximately half-way between the lakes on flat and generally sloping terraces and receives moderate mean annual rainfalls with cool temperatures (Table 1). *Agrostis capillaris* dominates the *F. novae-zelandiae* tussock grassland with low levels of *H. pilosella*. This area is also now managed by the Department of Conservation, without active management for agricultural grazing, although feral rabbits and hares graze the area.

The Cass Valley study site is located at the confluence of Alisa Stream and Cass River, consisting of alluvial flats. Similar to the South Branch of Hurunui River, this site's higher altitude and closer proximity to the main divide of South Island means that it has a high orographic rainfall (Table 1). The vegetation is *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland but with localised *A. capillaris* on damper soils. This site forms part of a summer grazing block for Glenmore Station, receiving light grazing of both sheep and cattle in the summer months, as well as grazing by wild ungulates (deer and thar) and feral hares year round.

Mt John, located west of Lake Tekapo, is a gently rolling moraine with a sub-humid climate (Table 1). The site's vegetation is a *H. pilosella* dominated *F. novae-zelandiae* short tussock grassland. It has a long history of sheep grazing and is adjacent to an AgResearch experimental trial established in 1982 examining various aspects grazing, fertilizer, irrigation and over-sowing on a *H. pilosella* invaded *F. novae-zelandiae* short tussock grassland (Scott, 1999); however, the specific study area has not received any of these treatments. Both feral rabbits and hares also graze this site.

Materials and Methods

Eleven 10.24m^2 vegetation plots were established at the four sites described above. Three plots each were established at Mt John, Cass Valley, South Branch of Hurunui, and a further two at Lyndon Road. Each of these plots was divided into 4096 twenty-five square centimetre subplots, forming a grid (64 x 64) (Figure 17). Within each of these subplots the dominant species (occupying the greatest space) was recorded, creating a pixelised map of the vegetation. Bare ground and dead vegetation were treated as pseudo-species. As spatial statistical methods assume stationarity, these plots were established in a pseudorandom method to ensure that environmental gradients within the plot were avoided, and trends detected were likely due to direct or indirect relationships between species. All plots were situated on flat, even terrain with vegetation distributed evenly over the entire plot.

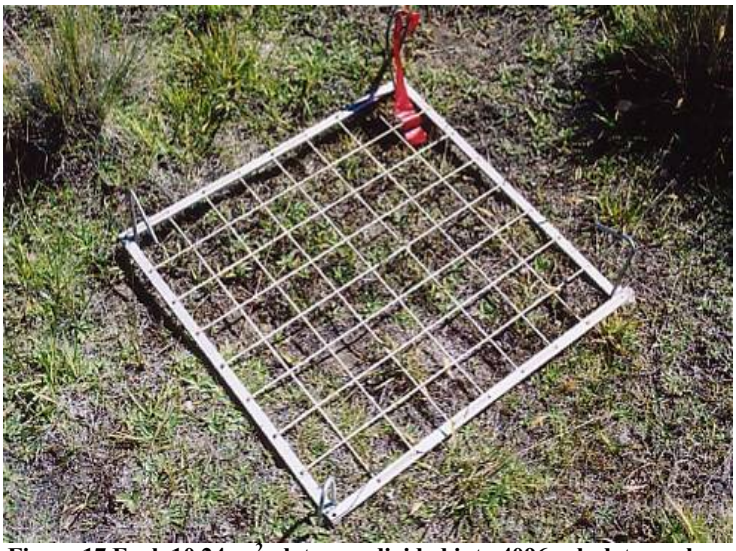

Figure 17 Each 10.24cm^2 plots was divided into 4096 subplots, each of them 25cm^2. The dominant species in each subplot was recorded. The 40cm x 40cm quadrat shown was used 64 times in a contiguous fashion to form a square plot, giving the correct size plot

Three similar analyses were carried out on this data examining the spatial patterns of species, life-forms (Table 5; Ellenberg & Mueller-Dumbois, 1967) and root functional groups (Chapter 4 and Table 5) The relationship of direct neighbours was examined using queens move join-count statistics (Appendix 1) (Cliff, 1970; Cressie, 1993; Dacey, 1968; Dale, 1999; Fortin & Dale, 2005; Upton & Fingleton, 1985) utilising the Sdep package in R 2.4.1 (R Development Core Team, 2006). Join-count statistics compare the number of different types of joins between cells to the expected value if the arrangement of cells is completely spatially random, giving a measure of aggregation, regularity or not significantly different from completely spatially random at scales between 5 and 7.07 cm. These scales were used because this is the distance between repeating units of contiguous and diagonal cells respectively. The types of joins are defined by the identity of both the adjoining cells, being either of the same species, or of two different specified species.

Table 5 Descriptions of Ellenberg and Mueller-Dombois's (1967) life-forms and root functional groups (Chapter 4) used in this research.

Life form	Description
Bulbous geophyte	Survival organs underground with bulbs or corms.
Caespitose hemicryptophyte	Herbaceous plants with periodic shoot reduction to a shoot system that lies relatively flat (c.f. tree life-forms) to the ground surface with bunched or circular shoot arrangement.
Frutescent chamaephyte	Woody dwarf shrub with mature shoot system which remains within 25-50cm above ground or who die back periodically to 25-50cm.
Herbaceous chamaephyte	Non-woody plant with mature shoot system which remains within 25-50cm above ground or who die back periodically to 25-50cm.
Phanerophyte	Taller than 25-50cm with woody stems and branches which do not die back periodically.
Reptant hemicryptophyte	Herbaceous plants with periodic shoot reduction to a shoot system that lies relatively flat (c.f. tree life-forms) to the ground surface with creeping or matted shoot arrangement.
Scapose hemicryptophyte	Herbaceous plants with periodic shoot reduction to a shoot system that lies relatively flat (c.f. tree life-forms) to the ground surface with a shoot arrangement which consists of a nearly or completely leafless flower stalk arising from a rosette.
Suffrutescent chamaephyte	Semi-woody dwarf shrubs with mature shoot system which remains within 25-50cm above ground or who die back periodically to 25-50cm. Woodiness restricted to the base of the shoot system.
Thallophyte	Non-vascular cryptogam, generally attached to the ground surface.
Therophyte	Annuals with an entire life cycle shorter than a year, usually within one favourable growing period.
Root Functional Group	**Description**
Cryptogam	No true roots, occupying only the soil surface.
Fibrous	Many adventitious roots arising from one area typically with dense branching.
Long dominant tap root	Long dominant tap root with well developed branching, occupying a large volume of soil.
Rhizomatous or stoloniferous	Roots arising from many nodes on horizontal stolons or rhizomes.
Short tap root with dominant deep laterals	Tap rooted species with dominating long thick almost vertical lateral roots which may reach great depths.
Short tap root with shallow laterals	Short tap roots with many longer horizontal laterals which branch to form a dense network of roots in the upper soil layers.
Weak	Few fine roots with or without tap root.

In order to examine patterns to scales larger than direct neighbours (5-7.07 cm), the grid data was also analysed following Fehmi and Bartolome's (2001) modified Ripley's *K*-function (Ripley, 1981, 1988) with isotropic edge corrections to describe each species' pattern as aggregated, regular or not significantly different from spatially random at a range of scales up to 160 cm. Ripley's *K*-function counts the mean number of points within a specified distance (scale) from every point, and compares this to the expected value of spatially random patterns at the same overall density. As the data is discrete rather than continuous (due to the use of grid based subplots), the distances which can be tested for aggregation and regularity are limited to those which correspond to the central point of the surrounding subplots. A Monte-Carlo process (100 binomial simulations) produced upper and lower significance envelopes, $\alpha = 0.02$ (Appendix 1). To ensure that the analysis was robust, only those species/life forms/root functional groups recorded within more than 30 subplots in the grid were analysed (Fortin & Dale, 2005). This modified Ripley's *K*-function was also extended to Ripley's K_{12}-function, to describe the spatial relationship between all the combinations of different species.

These spatial patterns were then grouped by similarity using a simple matching co-efficient unweighted pair group with arithmetic mean (UPGMA) hierarchical classification in MATLAB 7.0 (The MathWorks Inc., 2004) with aggregation, regularity or not significantly different from completely spatially random at each scale representing a single trait. An arcsine transformed analysis of variance (ANOVA) then determined if there were any significant differences in the proportion of subplots occupied by *H. pilosella* within the different types of patterns.

This grid-based methodology was used as many of the intertussock plants reproduce vegetatively; therefore, it is difficult to define the central point of a plant and to identify a single individual. This method also has the advantage of being able to provide information on the average plant or clump size as any aggregation at the smallest scales would indicate this.

Results

A total of 44 different species were detected amongst the plots, with an average of 16 species per plot. Plot 5 (Cass Valley) had the greatest species richness at 22, compared to the lowest species richness of just 7 in plot 8 (Lyndon Road).

The levels of *H. pilosella* in each plot varied from absent up to 55.1%, with the Mt John Site generally being more invaded than the other three sites (Table 6 and Appendix 4). The level of *H. pilosella* was highly variable at the Cass Valley site. *A. capillaris* also varied greatly among the plots, dominating the Lyndon Road site but was absent from plots at the South Branch of Hurunui River (although it is present in areas outside the plots).

Table 6 Cover of common vascular species (present in at least 50% of plots, as measured by the proportion of subplots which they dominate in each plot).

	Plot 2	Plot 3	Plot 5	Plot 1	Plot 4	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10	Plot 11
Hieracium pilosella	55.1%	54.9%	48.7%	40.7%	33.8%	7.9%	6.0%	1.5%	0%*	0%*	0%*
Agrostis capillaris	5.1%	4.0%	1.9%	5.5%	1.0%	13.5%	82.5%	92.4%	0%*	0%*	0%*
Anthoxanthum odoratum	0.8%	3.1%	4.3%	8.6%	3.8%	3.9%	2.5%	0.3%*	1.2%	3.7%	3.0%
Festuca novae-zelandiae	2.1%	3.6%	13.6%	3.3%	8.2%	10.0%	4.0%	4.1%	11.2%	16.6%	7.4%
Leucopogon fraseri	0.3%*	1.4%	5.7%	1.3%	23.9%	0%*	0%*	0%*	24.4%	11.1%	9.0%
Luzula rufa	0%*	0.2%*	3.3%	0.1%*	1.5%	2.0%	0%*	0%*	1.9%	2.2%	1.0%
Wahlenbergia albomarginata	0.4%*	0.2%*	2.8%	4.3%	1.6%	0.7%	0%*	0%*	0.4%*	2.5%	1.7%
Bare ground	15.6%	12.8%	0.1%*	7.0%	0.2%*	0.6%*	0%*	0%*	0%*	0%*	0%*
Dead Vegetation	8.0%	5.9%	1.0%	5.2%	1.9%	0%*	0.0%*	0%*	0%*	0%*	0%*

* less than 30 subplots

Species spatial patterns amongst direct neighbours

At the species level, patterns within and among species were generally weak with much variation between plots; however, several important trends were observed. Join-count statistics were used to examine the patterns of direct neighbours, at scales between 5 and 7.07 cm. These statistics indicated that most species are aggregated at this scale, as is bare ground and dead vegetation (Table 7).

Table 7 Join-count *Z*-scores of intra-species patterns of selected species

	Mt John			Cass Valley			Lake Lyndon		South Branch Hurunui		
Species	Plot 1	Plot2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10	Plot11
Agrostis capillaris	19.46*	14.11*	33.18*	4.06*	8.45*	9.17*	7.01*	8.70*	N/A	N/A	N/A
Anthoxanthum odoratum	16.13*	21.51*	10.50*	1.14	1.27	3.95*	11.16*	10.02*	5.56*	13.84*	4.09*
Festuca novae-zelandiae	63.49*	65.70*	51.77*	6.12*	4.97*	11.44*	19.42*	19.73*	13.46*	13.36*	10.35*
Geranium sessiliflorum	N/A	N/A	N/A	N/A	6.10*	6.28*	N/A	N/A	N/A	9.56*	7.02*
Hieracium pilosella	10.72*	28.30*	19.65*	0.70	2.84*	2.43*	9.71*	4.76*	N/A	N/A	N/A
Leucopogon fraseri	3.48*	N/A	7.90*	3.31*	6.50*	N/A	N/A	N/A	10.07*	7.46*	8.00*
Luzula rufa	N/A	N/A	N/A	2.55*	1.75	-0.14	N/A	N/A	8.10*	6.87*	7.91*
Trifolium repens	N/A	N/A	N/A	N/A	2.35*	2.83*	4.52*	3.95*	N/A	N/A	2.20*
Wahlenbergia albomarginata	8.28*	N/A	N/A	0.53	1.89	0.19	N/A	N/A	N/A	1.11	1.70
Bare ground	19.45*	32.78*	22.2*	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Dead Vegetation	10.51*	14.71*	8.81*	4.17*	2.77*	N/A	N/A	N/A	14.47*	9.90*	N/A

N/A less than 30 subplots are occupied by this species *Z-scores greater than 1.96 or less than -1.96 are statistically significantly (P=0.05) different from completely spatially random. Negative Z-scores show regularity, positive show aggregation.

The spatial relationships between species are more difficult to detect as there are few species combinations which are present in more than a handful of plots. The spatial relationship between *H. pilosella* and the dominant tussock species, *F. novae-zelandiae* is significantly regular at two of the sites; Mt John and Lake Lyndon ($P = 0.018$ and $P < 0.001$ in plots 8 and, 1, 2, 3, 7 respectively). At the Cass Valley site this regularity was not statistically significantly different from completely spatially random with ($P = 0.18$, 0.39 and 0.13 for plots 4, 5 and 6 respectively). Plots 9, 10 and 11 contain no *H. pilosella* subplots.

Similarly, the relationship between *H. pilosella* and *A. capillaris* is statistically significantly regular in plots 1, 2, 3 (all $P < 0.001$), 5 ($P = 0.009$) and 7 with ($P = 0.003$); however, plot 4 shows statistically significant aggregation ($P < 0.001$) and plots 6 and 8 are not significantly different from spatially random ($P = 0.861$ and 0.245). This should be compared with the spatial relationships between *H. pilosella* and *Anthoxanthum odoratum*, which are statistically significantly regular in only two plots ($P < 0.001$ in plots 1 and 3). The remaining plots are all not significantly different from completely spatially random ($P = 0.218$ to $P = 0.612$).

It is also interesting to note that the spatial relationship between *H. pilosella* and bare ground does not show a trend of aggregation for the three plots with a sufficient sample size, which would be expected if *H. pilosella* directly caused the bare ground. Significant regularity was detected in plots 2 and 3 ($P < 0.001$) and there was no significant difference from spatially random in plot 1 ($P = 0.083$).

A. capillaris, bare ground and dead vegetation are also generally regular with *F. novae-zelandiae*. It has significant spatial regularity with *F. novae-zelandiae* in plots 1, 2, 3, 6, 7, 8 ($P < 0.001$). Plots 4 ($P = 0.377$) and 5 ($P = 0.078$) are not significantly different from completely spatially random. Dead vegetation is regular with *F. novae-zelandiae* in Plots 1, 2, 3 (all $P < 0.001$), 9 ($P = 0.005$) and 10 ($P = 0.002$). Only plots 1 to 3 have more than 30 subplots each of bare ground and *F. novae-zelandiae*, however all three of these plots show regularity ($P < 0.001$).

None of the patterns detected within and between species by the join-count statistics differed significantly along the gradient of *H. pilosella* invasion.

Species spatial patterns beyond direct neighbours

Ripley's *K*-function generally agreed with these trends at scales of 5 to 7.07 cm, but found a variety of patterns at larger scales up to 160 cm . *H. pilosella* itself was found to be aggregated up to scales between 35 and 60 cm, and up to 135 cm at Lake Lyndon; much larger than an individual rosette (Figure 18). Five out of the eight plots with *H. pilosella* (6, 3, 5, 4, 1) also demonstrated regularity above 50-125 cm to the maximum scale measured 160 cm; however, of the remaining 3 plots (2, 7 and 8), plots 7 and 8 showed aggregation to much larger scales (*ca.* 140 cm), and none showed regularity at scales up to 160 cm. These patterns did not have any significant relationships with the level of *H. pilosella*.

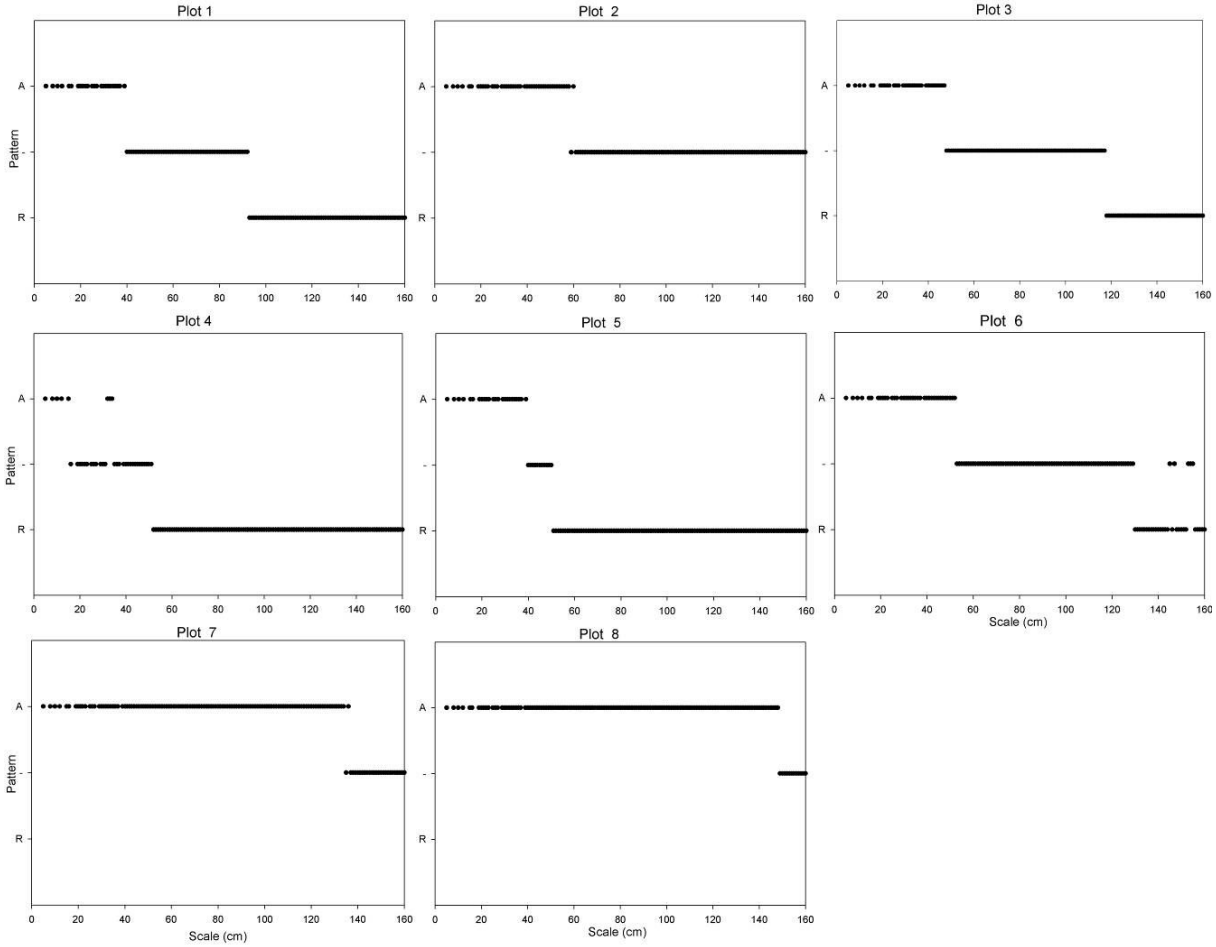

Figure 18 Pattern of aggregation (A), regularity (R) or not significantly different from spatially random (-) of *H. pilosella* at a range of scales up to 160 cm (α = 0.02).

The dominant tussock species, *F. novae-zelandiae*, demonstrated aggregation at scales up to between 60 and 126 cm, probably reflecting both individual tussock sizes but also ramets of the same plant, and clumping due to favourable microsites. Above this scale, four plots (2, 9, 10, 11), including all those in the South Branch of the Hurunui, show some regularity. The increasing scale of aggregation is significantly related to the overall amount of *F. novae-zelandiae* (P=0.006) but is unrelated to the level of *H. pilosella* (P=0.330).

Bare ground is clumped up to scales between 44 and 60 cm, with no significant difference from random in plots 1, 2 and 3. Similarly, dead vegetation is clumped up to between 15 and 112 cm in six out of seven plots, with no significant difference from random above these scales.

The only significant difference in pattern with the level of *H. pilosella* invasion was the increased aggregation of *A. capillaris* ($P<0.001$) (Figure 19 and Figure 20). At low levels of *H. pilosella*, *A. capillaris* is aggregated up to scales between 40 and 100 cm, with regularity above this scale. Where *H. pilosella* is high, *A. capillaris* is aggregated up to 145 cm or higher, with no detected regularity. The other common exotic grass, *A. odoratum* is aggregated up to scales between 26 and 130 cm, with patterns in 7 out of 10 plots not significantly different from random above this. Plots 6, 11 and 13 showed some regularity from scales above *ca.* 134 cm.

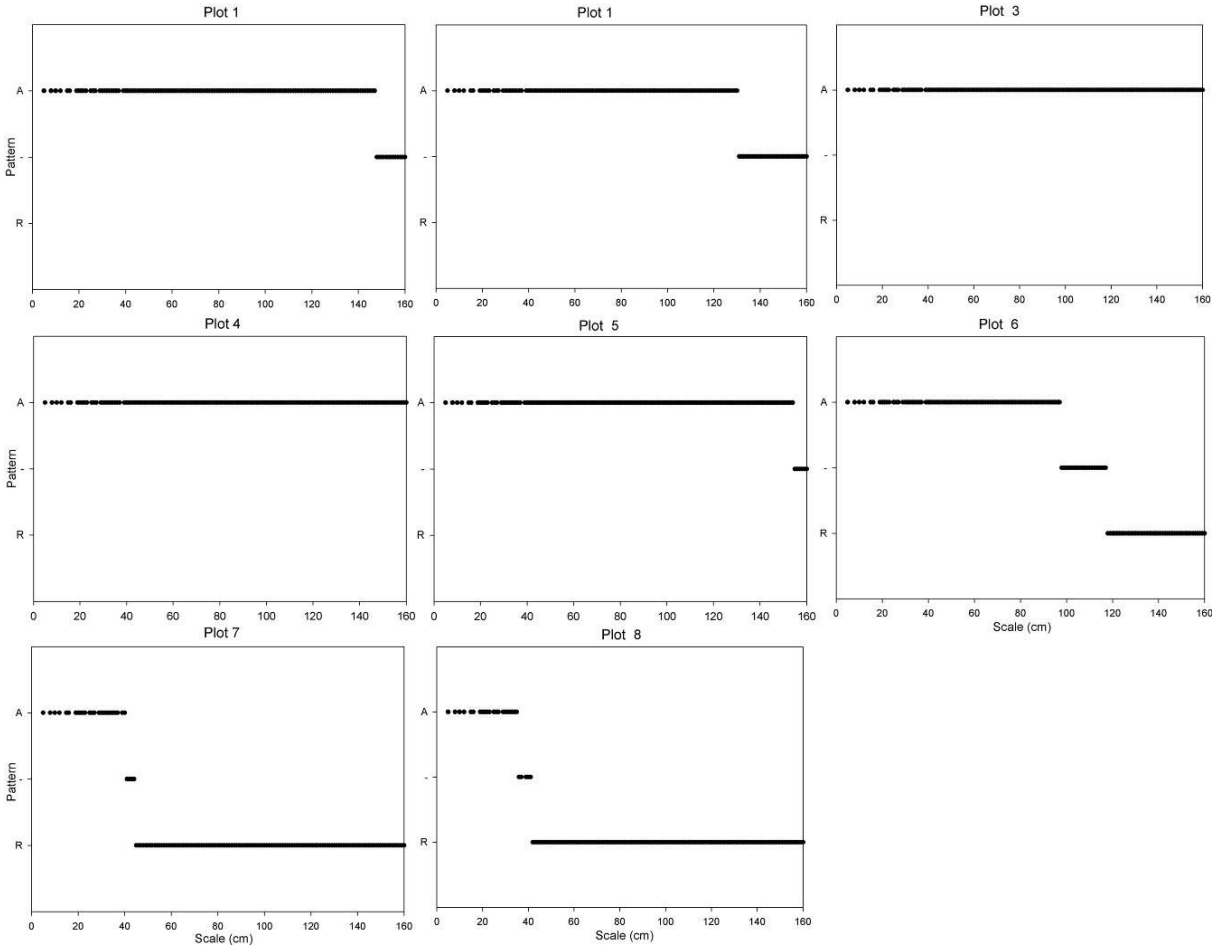

Figure 19 Patterns of aggregation (A), regularity (R) and not significantly different from spatially random (-) of *A. capillaris* in each plot.

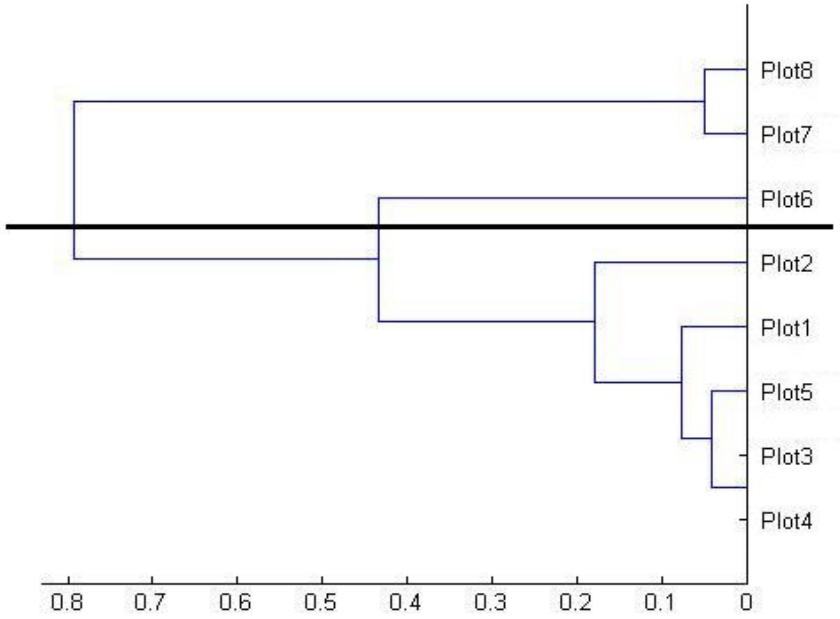

Figure 20 Dendrogram showing similarity between the spatial patterns of *A. capillaris* in each plot constructed utilising UPGMA hierachical classification with the simple matching coefficient. The bold horizontal line shows the cut off between two groups of patterns found in the plots

Three other common species exhibited aggregation across all plots where they were present, but without trends related to the level of *H. pilosella*. *Wahlenbergia albomarginata* was aggregated up to between 90 and 160 cm (the maximum scale examined) in plots 1, 4, 5, 6, 10 and 11, which is much greater than the size of a single rosette reflecting its rhizomatous nature. Similarly, *Leucopogon fraseri* was clumped up to a minimum 60 cm and maximum 150 cm in all 7 plots where it was present. *Luzula rufa* was aggregated up to scales of 64-100 cm in all 8 plots where it was present, in addition 3 of the 5 plots demonstrated some regularity above this.

The patterns between species identified by the Ripley's K_{12}-function were less consistent across scales and plots and the majority of patterns were not significantly different from completely spatially random across a variety of scales; although, some patterns did emerge.

Contrary to the join-count analysis, Ripley's K_{12}-function found that the relationship between *H. pilosella* and *F. novae-zelandiae* was not significantly different from spatially random at the

smallest scales in all plots. Due to the modifications made to Ripley's K_{12}-function to accommodate the use of grid subplots, the number of adjacent points which can be occupied at small scales is limited to the number of subplots that have midpoints within small distances (i.e. 4 subplots within 6 cm and 8 subplots within 9 cm); therefore it is thought that the join-count statistics would be more sensitive to the detection of these small scales between 5 and 7.07 cm. At least some regularity above these small scales was detected in plots 1, 3, 4, 5, 6 and not in plots 2, 7 and 8; however, this pattern was variable and not significantly related to the level of *H. pilosella*.

Similarly, Ripley's K_{12}-function did not detect any patterns significantly different from completely spatially random at the smallest scales between *A. capillaris* and *H. pilosella*, however the patterns at larger scales up to 160 cm do reflect those found in the join-count patterns. In plots 1, 2, 3, 5, 7 and 8, strong patterns of regularity were found; and aggregation was present between the two species up to 83 cm in plot 4.

The relationship between *H. pilosella* and *A. odoratum* was found to be regular at moderate scales (15-50 cm) in plots 1, 2, 3, 4, 5 and 7 compared to the completely spatially random patterns found in plots 6 and 8; although, not trends were significantly related to the level of *H. pilosella*.

Reflecting the results of the join-count analysis, *H. pilosella* and bare ground had neither consistently clear relationships nor trends up to scales of 160 cm. Also, *F. novae-zelandiae* and bare ground were regular at small to moderate scales (5-46 cm) in plots 2 and 3 but completely spatially random in plot 1. The relationship between dead vegetation and *F. novae-zelandiae* was also regular at small to moderate scales (5-70 cm) in most plots (1, 2, 3, 5, 9 and 10), being no different from completely spatial random in only plot 4. *A. capillaris* was found to be generally regular up to scales of 65 cm with *F. novae-zelandiae* in 5 out of 8 plots, with no significant trends across the *H. pilosella* gradient.

The only inter-species relationship which was found to differ significantly with the invasion of *H. pilosella* was between *Leucopogon fraseri* and *F. novae-zelandiae* (P<0.001) (Figure 21 and Figure 22). This relationship was increasingly regular at a range of scales when *H. pilosella* was at high levels.

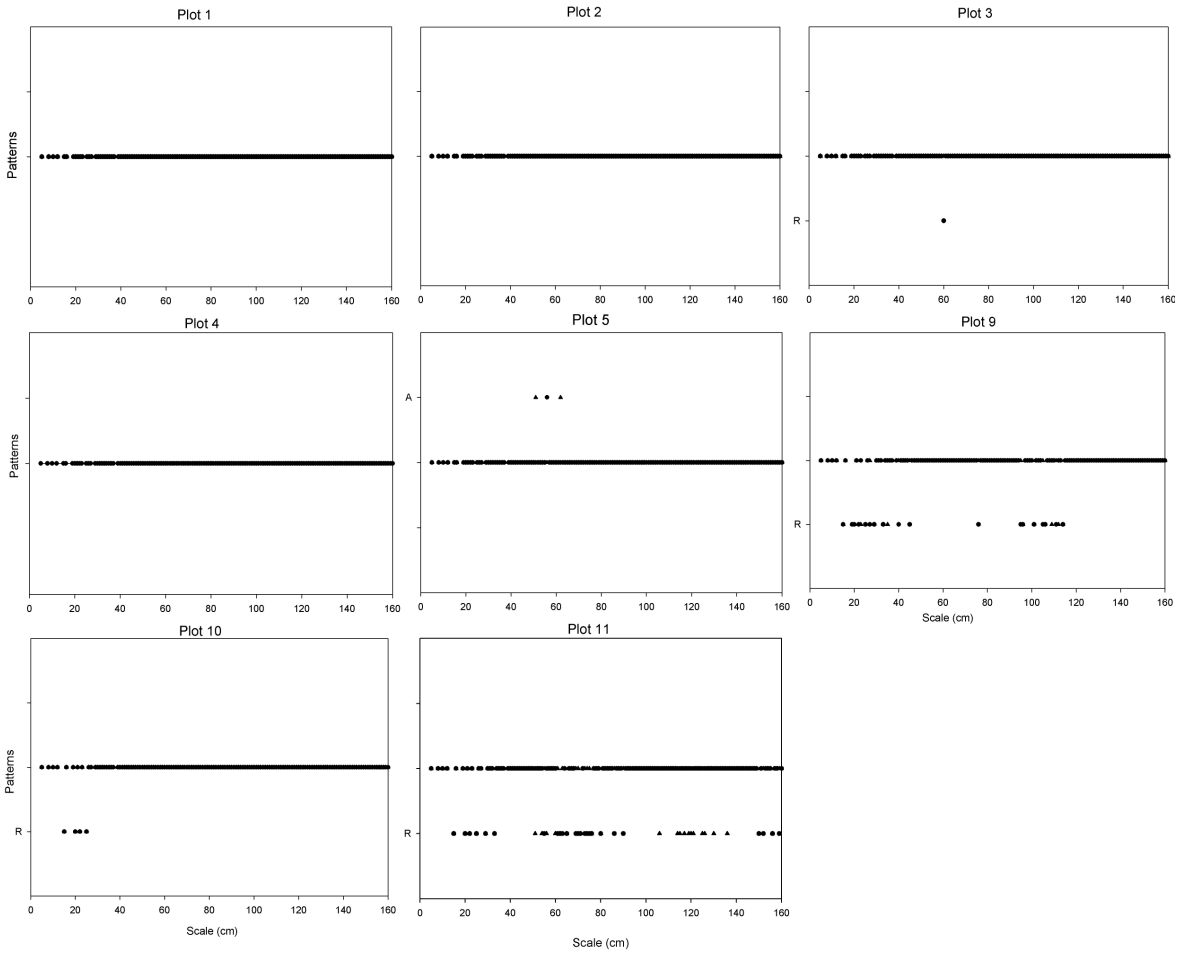

Figure 21 Patterns of aggregation (A), regularity (R) and not significantly different from spatially random (-) between *L. fraseri* and *F. novae-zelandiae* in each plot.

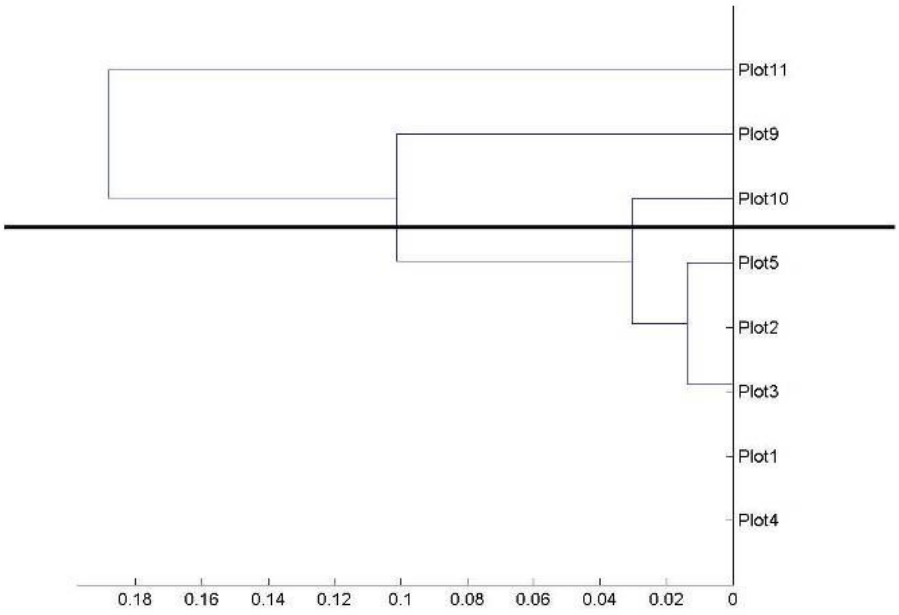

Figure 22 Dendrogram showing similarity between the spatial patterns of *L. fraseri* and *F. novae-zelandiae* in each plot. The bold horizontal line shows the cut off between two groups of patterns found in the plots, demonstrating increased regularity at high levels *of H. pilosella*

Life form spatial patterns amongst direct neighbours

When analysing this data using the life form groups of Ellenberg and Meuller-Dombois (1967) (Table 5 and Table 8), patterns of regularity and aggregation became more consistent and clearer. The join-count statistics showed that generally the life form groups were aggregated into clumps of similarity at scales between 5 and 7.07 cm reflecting the aggregation detected at the species level, with only two exceptions; bulbous geophytes in plot 1 and herbaceous chamaetophytes in plot 2, both of which were not significantly different from completely spatially random (P=0.91 and 0.15 respectively).

Table 8 Classification of species into life-forms (Ellenberg & Mueller-Dumbois, 1967) and root functional groups (Chapter 4)

Species	Life form	Root functional group
Acenea inermis	Herbaceous chamaephyte	Rhizomatous or stoloniferous
Agrostis capillaris	Caespitose hemicryptophyte	Fibrous
Anisotome aromatica	Scapose hemicryptophyte	Long Dominant tap root
Anisotome flexulosa	Scapose hemicryptophyte	Rhizomatous or stoloniferous
Anthoxanthum odoratum	Caespitose hemicryptophyte	Fibrous
Brachyglottis bellidioides	Herbaceous chamaephyte	Tap root with deep laterals
Carmichaelia vexillata	Frutescent chamaephyte	Long dominant tap root
Celmisia gracilenta	Caespitose hemicryptophyte	Short tap root with shallow laterals
Cerastium fontanum	Scapose chamaephyte	Short tap root with shallow laterals
Coprosma atropurpurea	Frutescent chamaephyte	Rhizomatous or stoloniferous
Copromsa perpusilla	Frutescent chamaephyte	Rhizomatous or stoloniferous
Discaria toumatou	Phanerophyte	Dominant tap root
Festuca novae-zelandiae	Caespitose hemicryptophyte	Fibrous
Geranium sessiliflorum	Suffrutescent chamaephyte	Dominant tap root
Hebe buchananii	Frutescent chamaephyte	Dominant tap root
Helichrysum filicaule	Herbaceous chamaephyte	Rhizomatous or stoloniferous
Hieracium caespitosum	Scapose hemicryptophyte	-
Hieracium pilosella	Scapose hemicryptophyte	Short tap root with shallow laterals
Hieracium praealtum	Scapose hemicryptophyte	Short tap root with shallow laterals
Holcus lantus	Caespitose hemicryptophyte	Fibrous
Hypochoeris radicata	Scapose hemicryptophyte	-

Leptinella spp.	Herbaceous chamaephyte	-
Leucopogon fraseri	Frutescent chamaephyte	Rhizomatous or stoloniferous
Linum catharticum	Scapose hemicryptophyte	Weak
Luzula rufa	Caespitose hemicryptophyte	Fibrous
Microtis oligantha	Bulbous geophyte	weak
Neuropogon cilliatus	Thallo-hemicryptophyte	Cryptogam
Ourisia spp.	Scapose hemicryptophyte	Short tap root with shallow laterals
Pimellea oreophila	Frutescent chamaephyte	Long dominant tap root
Poa colensoi	Caespitose hemicryptophyte	Fibrous
Poa maniototo	Caespitose hemicryptophyte	Fibrous
Poa novae-zealandiae	Casepitose hemicryptophyte	Fibrous
Polytrichum juniperinum	Thallo-hemicryptophyte	Cryptogam
Prasophyllum colensoi	Bulbous geophyte	weak
Pyrrhanthera exigua	Reptant hemicryptophyte	Rhizomatous or Stoloniferous
Racomitrium lanuginosum	Thallo-hemicryptophyte	Cryptogam
Ranunculus cheesemanii	Scapose hemicryptophyte	-
Raoulia subsericea	Herbaceous chamaephyte	Fibrous
Raoulia hookeri	Herbaceous chamaephyte	Fibrous
Rumex acetosella	Scapose hemicryptophyte	Rhizomatous or Stoloniferous
Scleranthus uniflorus	Herbaceous chamaephyte	-
Trifolium arvense	Therophyte	weak
Trifolium repens	Herbaceous chamaephyte	Rhizomatous or Stoloniferous
Viola cunninghamii	Scapose hemicryptophyte	-
Wahlenbergia albomarginata	Herbaceous chamaephyte	Rhizomatous or Stoloniferous

- root functional group is unknown; however, these species general make up a small proportion of the ground cover.

Join-count statistics also detected that frutescent chamaetophytes (woody dwarf-shrubs) and herbaceous caespitose hemicryophytes (tussocks) were statistically significantly regular in plots 1 ($P = 0.002$), 4, 6, 9, 10 and (all $P < 0.001$) and not significantly different from completely spatially random in plots 2, 3 and 5 (P = 0.34, 0.98 and 0.082). It was also found that thallophytes (non-vascular cryptogams) were generally regular with both caespitose hemicryophytes and scapose hemicryopytes (herbs with a leafless stalk rising from rosette-like leaves, including *H. pilosella*) (Table 9).

Table 9 Join-count z-scores of selected inter-life form patterns

	Mt John			Cass Valley			Lake Lyndon		South Branch Hurunui		
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10	Plot 11
thallophyte: caespitose hemicryptophytes	-8.85*	2.77*	-11.48*	-2.55*	N/A	N/A	N/A	N/A	-7.34*	-6.36*	-8.05*
thallophyte: scapose hemicryptophytes	-4.15*	-16.67*	N/A	-3.26*	N/A	N/A	N/A	N/A	-0.92	-1.56	-3.29*

N/A less than 30 subplots are occupied by this either life-forms. *Z-scores greater than 1.96 or less than -1.96 are statistically significantly (P=0.05) different from completely spatially random. Negative Z-scores show regularity, positive show aggregation.

Life form spatial patterns beyond direct neighbours

At larger scales, Ripley's K also found that all life forms examined, including frutescent, herbaceous and suffrutescent chamaephytes; caespitose, reptant and scapose hemicryophytes; and thallophytes, were generally auto-aggregated at small to moderate scales (from 5 cm, up to between 23 and 60 cm) reflecting the aggregation detected at the species level.

Two intra-life form patterns, as detected using Ripley's K, were found to have significant relationships to the level of *H. pilosella* invasion. Although all plots were aggregated at small scales, the maximum scale of aggregation in herbaceous chamaephytes decreased as the level of *H. pilosella* increased (P=0.01) (Figure 23 and Figure 24). At the same time, the scale of aggregation within scapose hemicryptophytes (which includes *H. pilosella*) decreased with increases in *H.*

pilosella (P<0.001). This decrease in the scale of aggregation is accompanied by an appearance of regularity at larger scales.

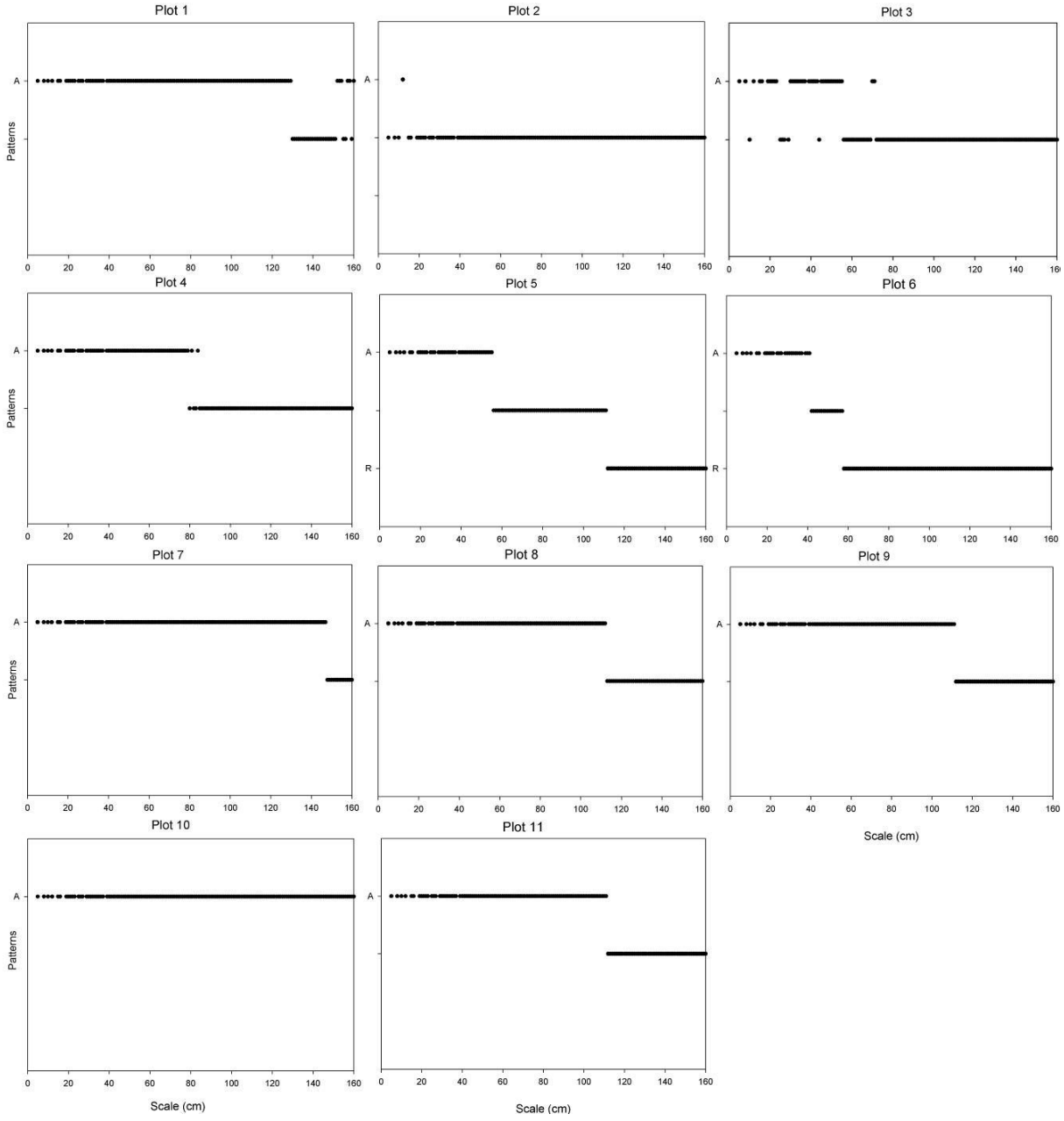

Figure 23 Patterns of aggregation (A), regularity (R) and not significantly different from spatially random (-) of herbaceous chamaephytes in each plot

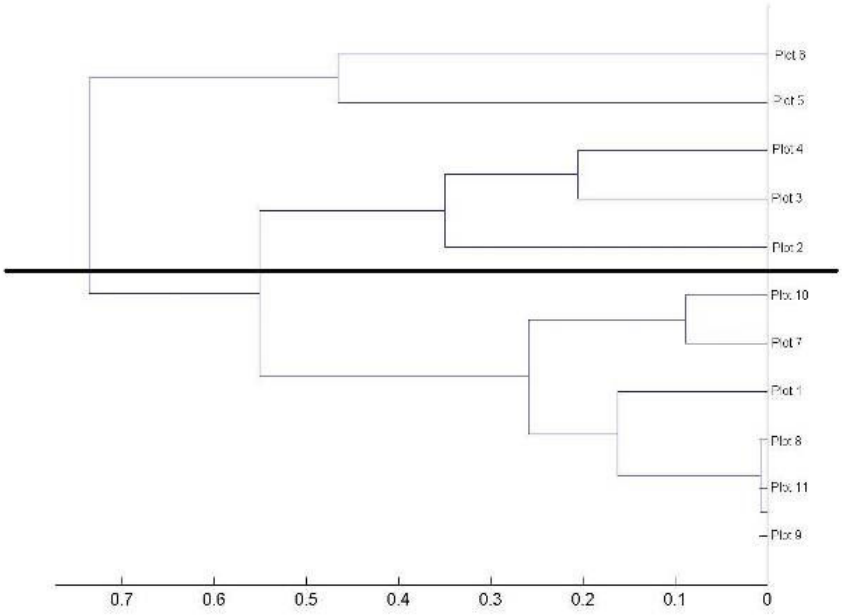

Figure 24 Dendrogram showing similarity between the spatial patterns of herbaceous chamaephytes in each plot. The bold horizontal line shows the cut off between two groups of patterns found in the plots.

Caespitose hemicryptophytes are also aggregated in all plots up to scales between 18 and 125 cm; however, plots with high *H. pilosella* invasion have a common pattern of regularity at larger scales ($P = 0.004$) (Figure 25 and Figure 26) . This significant relationship is compounded by a negative correlation ($R = -0.49$) between the level of *H. pilosella* and caespitose hemicryptophytes. Therefore plots with regularity at large scales also have significantly more caespitose hemicryptophytic cover ($P = 0.019$) .

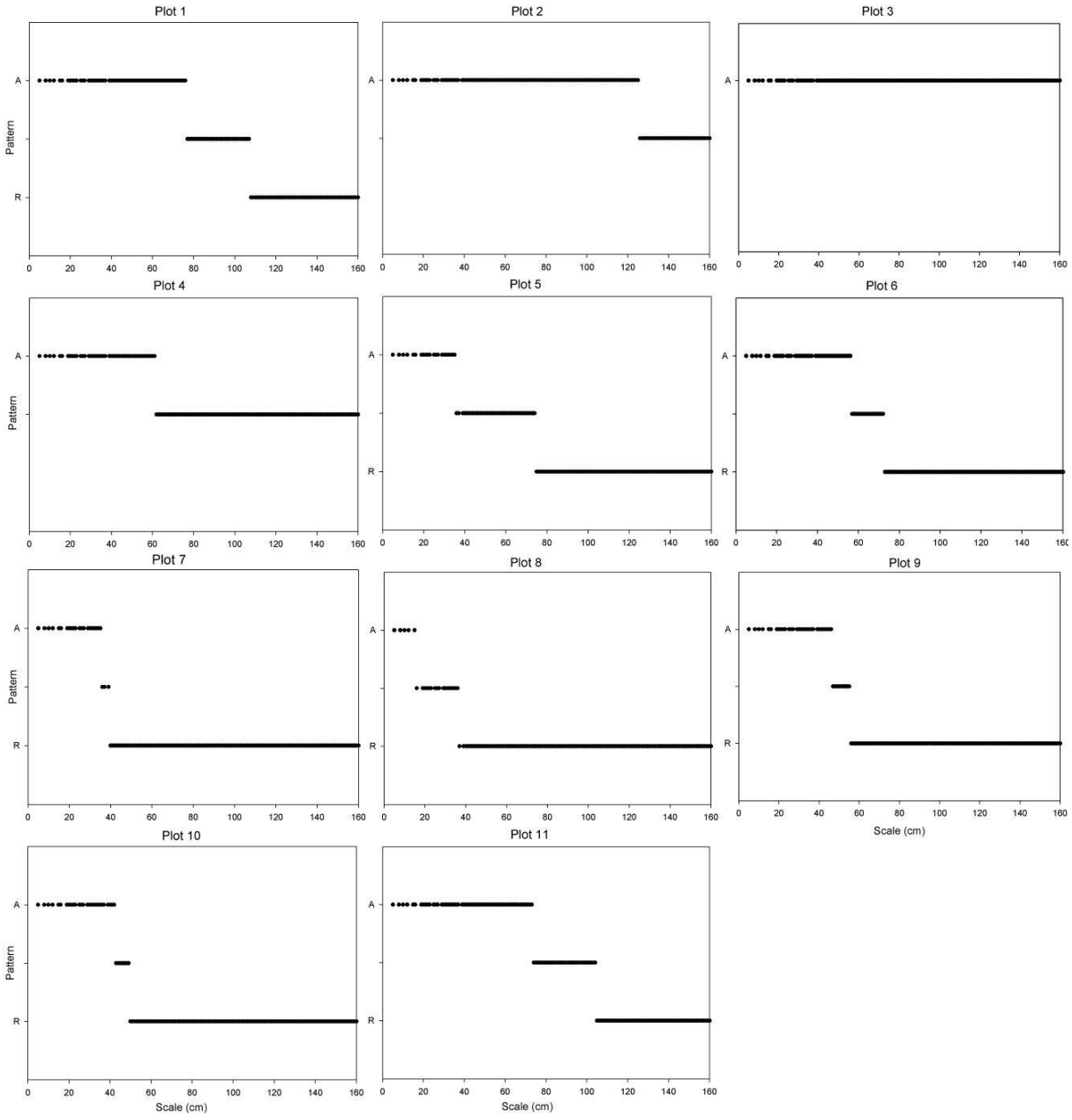

Figure 25 Patterns of aggregation (A), regularity (R) and not significantly different from spatially random (-) of caespitose hemicryptophytes in each plot.

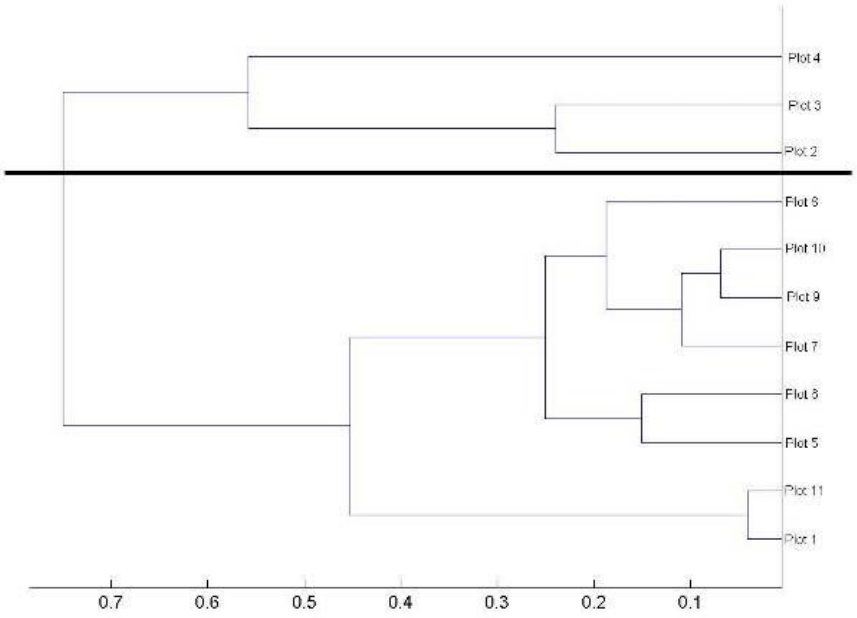

Figure 26 Dendrogram showing similarity between the spatial patterns of caespitose hemicryptophytes in each plot. The bold horizontal line shows the cut off between two groups of patterns found in the plots

Several significant changes were also observed using Ripley's K_{12}-function in the spatial relationships between life-forms with the increase in *H. pilosella*. There is decreased regularity between frutescent chamaephytes and thallophytes ($P = 0.026$); caespitose hemicryptophytes and thallophytes ($P = 0.008$); and frutescent chamaephytes and caespitose hemicryptophytes ($P = 0.004$) with increases in *H. pilosella*. There is also an increasing regularity between frutescent chamaephytes and scapose hemicryptophytes ($P < 0.001$); scapose hemicryptophytes and dead vegetation ($P = 0.002$); caespitose hemicryptophytes and scapose hemicryptophytes ($P = 0.009$); and herbaceous chamaephytes and scapose hemicryptphytes ($P = 0.002$). The patterns between frutescent chamaephytes and herbaceous chamaephytes also changed with significant increases in *H. pilosella*, to become less significantly different from random demonstrating a weakening of the spatial relationship (P=0.006)

Outside of the patterns described above, regularity at small scales was detected across the gradient of *H. pilosella* invasion in almost a dozen other relationships including: casepitose

hemicryptophytes and reptant hemicryptophytes; scapose hemicryptophytes and suffrutescent chamaephytes; scapose hemicryptophytes and thallophytes; scapose hemicryptophytes and reptant hemicryptophytes; caespitose hemicryptophytes and scapose hemicryptophytes; herbaceous chamaetophytes and caespitose hemicryptophytes; reptant hemicryptophytes and dead vegetation; and thallophytes and dead vegetation.

Root-functional group spatial patterns amongst direct neighbours

To determine the spatial relationships of different root morphologies, the root functional groups of Chapter 4, were also applied to the data (Table 5 and Table 8). Similar to the species and life form analyses; join-count statistics indicated that all the root functional groups (cryptogams, dominant tap root, fibrous, rhizomatous and stoloniferous, short tap root and shallow lateral, and tap root with deep laterals) were spatially aggregated at scales between 5 and 7.07 cm, except for those which were weakly rooted. Weakly rooted plants were not significantly different from completely spatially random in plots 1, 4, 6 ($P = 0.890, 0.853, 0.202$ respectively) and aggregated in plot 2 ($P < 0.001$). The join-count statistics also indicate that there are several patterns of significant regularity between root functional groups at this scale (Table 10).

Table 10 Join-count z-scores of selected inter-root functional group patterns

	Mt John			Cass Valley			Lake Lyndon		South Branch Hurunui		
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10	Plot 11
fibrous:bare ground	-10.38*	-10.45*	-11.06*	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
fibrous:Cryptogam	-8.96*	2.77*	-5.14*	-3.35*	N/A	N/A	N/A	N/A	-7.34*	-6.36*	-8.02*
rhizsomatous and stoloniferous: fibrous	-6.46*	-0.19	-5.37*	-3.99*	-3.58*	-3.99*	-2.54*	-2.20*	-5.57*	-8.39*	-4.79*
short tap root and shallow lateral: cryptogam	-4.15*	-17.09*	-14.69*	-3.02*	N/A	N/A	N/A	N/A	N/A	N/A	N/A
short tap root and shallow lateral: fibrous	-11.89*	-12.32*	-10.74*	0.67	-0.38	-1.22	-6.20*	-3.10*	N/A	N/A	N/A

N/A less than 30 subplots are occupied by this either life-forms *Z-scores greater than 1.96 or less than -1.96 are statistically significantly (P=0.05) different from completely spatially random.
Negative Z-scores show regularity, positive show aggregation.

Root functional group spatial patterns beyond direct neighbours

On examining the spatial patterns within and between root functional groups at scales up to 160 cm using Ripley's *K*-function, we observed two intra-functional group patterns which differ between levels of *H. pilosella* invasion were observed. Fibrous root systems were aggregated in all plots at small scales; however where *H. pilosella* levels were low, regularity also occurred at large scales ($P = 0.004$). In contrast, short tap rooted plants with shallow laterals had regularity at large scales where *H. pilosella* was high ($P < 0.001$). These two patterns reflect those seen earlier in their corresponding life-forms; caespitose hemicryptophytes and scapose hemicryptophytes respectively.

Four patterns between root functional groups, which differ significantly with levels of *H. pilosella* invasion, were also detected using Ripley's K_{12}-function. Fibrous rooted and Cryptogam plants were regular at small scales in all plots, however the maximum scale of this regularity increased with high levels of cryptogams ($P = 0.010$) and low levels of *H. pilosella* ($P < 0.001$); however, the level of *H. pilosella* and cryptogams were only weakly positively correlated ($R = 0.21$). Dominantly tap rooted and fibrous rooted plants also had a similar spatial relationship, with regularity observed in all plots at small scales but the maximum scale of regularity was larger where the level of *H. pilosella* was low (P=0.02). In contrast, the small scale (*ca.* 30 cm) regularity which was observed in the spatial relationship between rhizomatous and stoloniferous and short tap and shallow lateral plants, and rhizomatous and stoloniferous and dead vegetation increased in scale with increases in the level of *H. pilosella* ($P = 0.037$ and 0.040 respectively).

The Ripley's K_{12}-function also highlighted many relationships which were regular at small to moderate (up to *ca.* 25 cm) scales but without any significant trend across the *H. pilosella* invasion gradient. These included: cryptogam and rhizomatous/stoloniferous; cryptogam and short tap root with shallow laterals; fibrous and dead vegetation, fibrous and bare ground; fibrous and short tap root with shallow laterals, cryptogam and dead vegetation; dominant tap root and short tap with shallow laterals, dominant tap root and rhizomatous/stoloniferous, rhizomatous/stoloniferous with

cryptogam; rhizomatous/stoloniferous and dead vegetation; rhizomatous/stoloniferous and fibrous; cryptogam and bare ground; and dead vegetation and short tap root with shallow laterals. Only the weakly rooted plants showed no clear trends or patterns with any other root functional group, being either not significantly different from spatially random or variable between plots.

Discussion

The results show that there are consistent statistically significant small scale spatial structuring of the plant species within these short tussock grassland communities, particularly at the level of life-forms and root functional groups. This spatial structuring is typically characterised by aggregation at small scales (up to *ca.* 40cm) within species, life forms and root functional groups, and regularity between species, life forms and root functional groups; although, randomness remains a strong feature. This aggregation at small scales may be a facet of the methods used here, where the average size of the species is greater than the 25 cm^2 sampling unit (e.g. *A. capillaris*, *F. novae-zelandiae* and *L. fraseri*) or indicative that vegetative reproduction is important (e.g. *W. albomarginata*). However, the presence of aggregation within other species, life forms and root functional groups, where these factors are not important (e.g. the non-vascular mosses and lichens, *T. arvenses*, and *B. bellidioides*), indicates that some other process is affecting the spatial patterns such as strong microsite preferences. Where a limiting resource is strongly heterogeneously patchy within a site, individuals of specific species, life forms or root functional groups may only germinate and survive within favourable patches, forming patterns of aggregation within a scale dictated by the size of the resource patches. This small scale aggregation also supports previous work (Murrell *et al.*, 2001; Potthoff *et al.*, 2006; Stoll & Prati, 2001; Turnbull *et al.*, 2007) which suggests that intra-specific aggregation reduces contact with other species and therefore reduces inter-specific competition. These results disagree with Walker and Langridge (2002), who conclude that "...individuals within a life form do not interact with each other as much as they do with other life forms" and "... it is more likely that a plant of one life form will be juxtaposed with plants of different life forms". These statements suggest that intra life form (including species and

root functional group) patterns should be random or regular at the smallest scales relative to plant size, and differing life forms will be direct neighbours in either a random or alternating pattern, which contradicts the conspecific aggregation detected in Turnbull *et al.* (2007); Murrell, Purves and Law (2001); and our results.

The results presented here also show that *H. pilosella* is altering the patterns of some species, life form and root functional groups, causing structural fragmentation; although, not all groups were affected and those affected were altered in different ways. For example both *A. capillaris* and herbaceous chamaephytes exhibited statistically significant increased aggregation with increases in *H. pilosella*. In contrast, increased regularity at scales greater than 40 cm was detected between tussocks in plots with high levels of *H. pilosella*. The relationships between some groups have also been affected by *H. pilosella* invasion. Some inter-group patterns have increased maximum scales of regularity where *H. pilosella* is at high levels, perhaps indicating the establishment of *H. pilosella* between them forcing increased regularity, for example the spatial relationships between *L. fraseri* and *F. novae-zelandiae*, and between scapose hemicryptophytes (which includes *H. pilosella*) and frutescent chamaephytes, dead vegetation, caespitose hemicryptophytes and herbaceous chamaephytes. The relationship between other groups have decreasing maximum scales of regularity (or increased randomness) with high levels *H. pilosella* perhaps indicating that one or both groups are being replaced by *H. pilosella*, weakening the spatial relationship between them. This is an indication that one or both these species are only weakly competitive against *H. pilosella*. Examples of this decreased regularity, or increased spatial randomness include the spatial relationships between frutescent chamaephytes and thallophytes, casepitose hemicryptophytes and thallophytes (or fibrous rooted plants and cryptogams), frutescent chamaephytes and caespitose hemicryptophytes, and frutescent chamaephytes and herbaceous chamaephytes.

Scott (1959; 1961) focused on the spatial relationships of inter-tussock species with tussocks. He found that tussocks modified their surrounding environment and dictated the spatial patterns of particular species as they formed concentric circles centred on the tussocks with differing mean radii. In agreement with Scott's (1959; 1961) conclusions, the regularity between tussocks and both bare ground and dead vegetation indicates that tussocks probably have a generally favourable affect on the vegetation around them. These relatively large gaps of either bare ground or dead decomposing vegetation should be quickly monopolised in conditions favourable for vegetation by either newly established individuals or the expansion of neighbours. The absence of these large gaps near tussocks implies that either the response of regeneration and neighbours which would normally fill these gaps is faster adjacent to tussocks than further away from tussocks, or that fewer gaps open-up through the death of individuals near tussocks. However, the results presented here show no evidence of aggregation or facilitation between tussocks and specific inter-tussock species up to scales of 160 cm. Regularity between tussocks and a handful of inter-tussock species, including *H. pilosella*, *A. capillaris* and *L. fraseri*, was found at various scales demonstrating that the tussocks are modifying the environment. The presence of regularity is indicative of a competitive or negative effect between tussocks and these species, as the strongest competitor prevents the germination and/or survival of the other species in adjacent areas. This research confirms Scott's (1959; 1961) observations that species differ in their spatial response to tussocks.

Inter-specific regularity between *H. pilosella* and *F. novae-zelandiae* at both the Mt John and Lake Lyndon sites suggests there is a competitive exclusion effect occurring as one species prevents the germination and/or survival of the other in adjacent areas. As *F. novae-zelandiae* is part of the pre-invasion vegetation, it is assumed that it is the tussocks which are excluding the invasive *H. pilosella*, providing some resistance to the invasion. Both of these sites are drier than the Cass Valley site with mean annual rainfalls of *ca.* 600 mm and 1000 mm respectively, compared to Cass Valley's mean annual rainfall of *ca.* 2000 mm. The tussocks may directly outcompete the shallowly rooted *H. pilosella* (Chapter 4 and Bishop & Davy, 1994) for soil resources (particularly

moisture), or may indirectly affect them by altering surrounding microsites through shading. The affect of shading from overhanging vegetation (such as tussocks) on *H. pilosella* has also been implicated elsewhere (Bishop & Davy, 1994; Rose & Frampton, 1999).

H. pilosella is classed as a scapose hemicryptophyte, and the clumping of scapose hemicryptophytes at low levels of invasion demonstrates that *H. pilosella* invades into favourable sites and then spreads from these sites into neighbouring areas. These favourable sites are likely to be adjacent to other species of scapose hemicryptophytes (for example, *Ranunculus cheesemanii*, *Brachyglottis bellidioides* and *Anisotome aromatica*), as this statistically significant decrease in aggregation of scapose hemicryptophytes is not significant when examining *H. pilosella*'s patterns in isolation.

The strong patterns of aggregation and regularity detected within common species including *H. pilosella*, *A. capillaris* and *F. novae-zelandiae* indicate that Turnbull *et al.*'s (2007) prediction that common species will have weak spatial structure due to their occupation of a high proportion of the ground cover does not apply to these short tussock grasslands. Also, only *F. novae-zelandiae* and *H. pilosella* demonstrate regularity at larger scales when they are at statistically significant higher densities. This regularity is a good indication of intra-specific competition occurring where these species occupy a high proportion of the ground cover. At a 'saturation point' with high proportions of ground cover (probably near their maximum site occupancy) *F. novae-zelandiae* and *H. pilosella* can no longer avoid intra-specific competition through the lack of conspecific neighbours in a random pattern. A pattern of regularity emerges as the minimum distance between conspecifics which allows coexistence becomes the normal distance between them, and regular gaps between plants are formed by the tight packing of individuals.

The halo effect of *H. pilosella* is well recorded (McIntosh *et al.*, 1995). It is the absorption of nutrients and moisture from an area surrounding the *H. pilosella* patch, causing a halo of bare-ground where other species do not survive to form around the *H. pilosella* patch. The results

presented here do not show a clear aggregation between *H. pilosella* and bare ground at small scales, which would be expected if the halo effect had an impact at these sites, demonstrating that while it may be important on some sites as reported elsewhere, it is not generally applicable to all sites and that the presence of bare ground is not intrinsically linked to *H. pilosella*. Another explanation for for this halo effect at some sites but not others may also reflect a minimum *H. pilosella* patch size before the patch begins to form a halo. This is reflected in the *H. pilosella* patch sizes where a halo pattern is detected.

The structural fragmentation detected in this research is likely to have flow-on effects for these species and their faunal communities. Changes in the spatial pattern of these species may affect the behaviour of pollinators, wind pollination, herbivore, and predator prey interactions, particularly of small invertebrates. Similarly, the spatial patterns of host organisms are also important to the success of bio-control agents introduced (Real & McElhany, 1996). In an investigation into a white rust (*Puccinia hieracii* var. *piloselloidarum*) introduced into New Zealand to control *H. pilosella*, Jenkins (1995) suggested that the local density of *H. pilosella*, its spatial patterns and neighbours may be important to the spread of the rust as tall grasses may act as a shield. Where sites have very high *H. pilosella* ground covers and low levels of caespitose hemicryptophytes, such as Mt John, spatial patterns a probably not critical to the spread of white rust; however at sites such as Lyndon road, with high levels of grass cover, spatial patterns are likely to be important. The results presented here demonstrates that the level of aggregation is higher at Lyndon Road than Mt John or Cass Valley, indicating clumps of *H. pilosella* are larger, however only scales up to 160 cm were observed. It is likely that the gap between clumps is also larger (regularity at scales larger than 160 cm), particularly as the total cover of *H. pilosella* within these plots is lower, and that this larger gap with the dominance of grass cover would prevent the establishment and survival of an effective white rust population.

Spatial patterns of pre-invasion vegetation and establishing *H. pilosella* populations as discussed above are likely to contribute to the success of *H. pilosella* invasion; however, the biology of this invasion is complex and there is no single reason why it has been so successful (Platt *et al.*, 1995). As *F. novae-zelandiae* is the only species to have shown some resistance against the invasion of *H. pilosella*, maintaining a cover of these tussocks may be important to prevent further invasion and degradation by *H. pilosella*.

This chapter aimed to 1) determine if there are consistent spatial patterns in New Zealand's short tussock grasslands at relatively small scales; 2) investigate how the invasion of *H. pilosella* may be altering these spatial patterns; and 3) establish if the spatial patterns of species, life-forms and root functional groups are being altered in different ways. It was found that; there are consistent spatial patterns in New Zealand's short tussock grasslands at relatively small scales; the invasion of H. *pilosella* is altering these spatial patterns; and, the way in which *H. pilosella* alters the spatial patterns of species, life-forms and root functional groups differs between those groups depending on their ecology and competitive interactions with *H. pilosella*.

Chapter 6

Discussion and Conclusions

This thesis has demonstrated that there are broadly consistent small-scale patterns of species, life-forms and root functional groups across a range of short tussock grasslands. In Chapter 2 the dominant tussock species, *Festuca novae-zelandiae,* consistently showed a pattern of regularity or randomness at small scales less than 50 cm in all plots, followed by aggregation at some greater scale up to 500 cm in 14 out of 15 plots. This regularity at small scales is a result of both the average size of tussocks (as an estimated central point was used for locating tussocks) but also competition between individual tussocks. The aggregation at greater scales is indicative of microsite preferences in a heterogenous environment, as Lord's (1992) study indicates that it is unlikely to be familial groups resulting from vegetative reproduction. Chapter 5 also supports these results indicating aggregation of *F. novae-zelandiae* subplots at small scales as the mean tussock basal area is larger than a single subplot, and regularity or not significantly different from random at larger scales (up to 160 cm). A general trend within species, life-forms and root functional groups of subplot aggregation at the smallest scales, with some regularity and randomness at greater scales was also detected although it differed between groups e.g. *H. pilosella*, *Luzula rufa*, and caespitose hemicryptophytes (Chapter 5).

Consistent spatial relationships between species, life forms and root functional groups were also detected. The most common spatial pattern between groups was regularity at small scales (up to *ca.* 70 cm), including caespitose hemicryptophytes and reptant hemicryptophytes, caespitose hemicryptophytes and scapose hemicryptophytes, scapose hemicryptophytes and thallophytes (Chapter 5). It is important to note that these spatial relationships between species, life forms and root functional groups demonstrate competition (regularity) and indifference (spatial randomness) only, no facilitation (aggregation) between groups was detected.

The strong spatial relationships between tussocks and other species supports the conclusions of Scott (1959; 1961) that tussocks modify the spatial patterns of other species in short tussock grasslands. However, these results do not show facilitation between tussocks and any other species, merely the presence of competition giving regular spatial patterns and indifference producing random spatial patterns. These results agree with Turnbull *et al.* (2007) and Murrell, Purves and Law (2001) that spatial patterns are important to competitive interactions and all species are aggregated at some level, with individuals interacting with conspecifics more often than would be expected from their overall abundance. However, this conflicts with Walker and Langridge's (2002) suggestion that individuals are more often juxtaposed with individuals of different life-forms, being complementary in their resource use. This aggregation may be due to phenological variation within species allowing for coexistence, and within species preferences for particular microsites superseding competitive effects between intra-specific individuals.

It has also been shown that the level of *H. pilosella* is related to the spatial patterns of plant species in South Island's short tussock grasslands. This is a strong indicator that *H. pilosella* is causing structural fragmentation. The exact nature of this fragmentation is variable between species, life-forms and root functional groups. For example, both *A. capillaris* and herbaceous chamaephytes have increased aggregation with increases in *H. pilosella* cover; however, tussocks had increased regularity at scales up to 160 cm (Chapter 5) and increased aggregation at large scales up to 500 cm (Chapter 2). The relationships between species, life-forms and root functional groups are also being altered in a differential manner. There was an increase in the maximum scale of regularity between *L. fraseri* and *F. novae-zelandiae* with increases in *H. pilosella*; in contrast, the relationship between frutescent chamaephytes and thallophytes had a decrease in the maximum scale of regularity (Chapter 5). These differences in the effect of *H. pilosella* on the spatial patterns of short tussock grasslands probably reflect differences in competitive interactions between *H. pilosella* and the various species, life-forms and functional groups.

This structural fragmentation may act as a ratchet in the invasion of *H. pilosella*, promoting further invasion and fragmentation. Fragmentation of tussocks and other vegetation by *H. pilosella* opens up the vegetation and modifies microsite environments, encouraging *H. pilosella* regeneration and perhaps preventing native species regeneration. Although this ratchet effect may escalate the invasion of *H. pilosella*, in isolation it does not fully explain the success of this invasion.

Furthermore, this fragmentation is likely to have far reaching consequences on both the flora and fauna of these communities. It is likely to lead to a break down of their traditional habitat, and alter the availability or quality of its resources; however the impact of these changes is unknown. Some species may benefit from these changes in habitat, while others suffer depending on their specific needs; moreover, fragmentation is thought to affect organisms with specialist behaviours more than generalists (Lord & Norton, 1990).

New Zealand's native alpine and subalpine plants, including species found in short tussock grasslands, are on the whole pollinated by generalists such as flies (Primack, 1983) and therefore the fragmentation of their habitat is not thought to be important,; however, many pollinators are known to act in a density dependent manner (Ghazoul, 2005) preferentially visiting types of flowers which are locally common even though many other types of flowers may be present. The dominance of showy yellow *H. pilosella* flowers inter-dispersed with native flowers may therefore alter the behaviour of these generalist pollinators. Timing of *H. pilosella* and other species' flowering flushes is also important, as pollen resources are highly seasonal in these environments. Any changes in pollination are likely to result in changes to the quantity and quality of seed produced, and therefore affects the regeneration of native entomophilous species. Changes in the behaviour and composition of the pollinator community are also likely to affect the behaviour and composition of their predators; therefore the structural fragmentation of short tussock grasslands will have even further flow-on effects throughout the ecosystem. Changes in spatial patterns of wind pollinated tussocks may also affect their pollination (Davis *et al.*, 2004).

This thesis sought to understand spatial aspects of short tussock grassland ecology, and did not seek definitive solutions to the invasion of *H. pilosella* in New Zealand's short tussock grasslands; however, the results suggest that the maintenance of a dense short tussock cover and the promotion of taller vegetation such as shrubs and tall tussock species are important in resilience against *H. pilosella* (Chapter 5). Solutions suggested elsewhere such as consistent long-term fertilisation and irrigation (Bishop & Davy, 1984a; Norton *et al.*, 2006 ; Rose *et al.*, 1998; Scott, 2001; Scott & Jenkins, 2006) are likely to be effective but are impractical over large areas of dry infertile lands, and will reduce native biodiversity values (Moen & Meurk, 2001; Scott, 1993, 2000; Scott *et al.*, 1990b 219). As such the promotion of taller, dense vegetation should play a role in planning for the control of *H. pilosella*.

The importance of below ground interactions in these short tussock grasslands should not be neglected. Despite difficulties in studying root systems, and separating the effect of below and above ground competition, Chapter 4 provides a classification which may be a useful tool in studies of below ground competition. It was hoped that by studying the spatial patterns of life-forms and root functional groups separately, the importance of studying below ground interactions in providing insights into the effect of root structures on competitive interactions would be highlighted. The study of root functional groups found that the relationships between fibrous root systems and rhizomatous and stoloniferous were significantly regular at small scales. This regularity indicates there is some-sort of competitive effect between these two types of root functional groups. As both of these functional groups tend to be far reaching, at a variety of depths it is likely that they do not divide the resources spatially and are competing for the same resources. The shading effect of taller dense vegetation on surrounding individuals has been implicated in the spatial regularity between caespitose hemicryptophytes and other plants; however the competition between the dense network of tussock and grass roots below ground may also be important.

On a general level, these results indicate that spatial relationships are important in ecological studies, in agreement with a growing body of spatial ecology literature (Curtis, 1955; Dale, 1999; de Broeck *et al.*, 2006; Fortin & Dale, 2005; Legendre, 1989, 1993; Sokal & Oden, 1978; Tilman & Kareiva, 1997; Turnbull *et al.*, 2007). The spatial arrangement of plants in particular dictates who they mainly interact with, and what resources are available for exploitation. As such, spatial patterns at a variety of scales should be considered in most plant ecological studies and not simply ignored or treated as a statistical nuisance.

The studies carried out as part of this thesis have also highlighted the usefulness of life-form and functional groups for analysing data from a range of sites and communities. Studies of these spatial patterns using taxonomic groupings only would have failed to find strong patterns, and probably resulted in incorrect conclusions that spatial patterning is on the whole not important in these plant communities. Although life-forms and functional groups are largely subjective, they are a useful way of organising life-forms into groups which act in generally similar ways given the attributes of interest.

Future work

As Turnbull *et al.*'s (2007) work has previously demonstrated, the effect of spatial structure on competitive interactions may change between years, most likely as a result of changes in the environment. The research undertaken in this thesis is a snapshot of the spatial arrangements in a gradient of sites at one point in time. However, further work remeasuring and analysing the spatial arrangement of plants in permanent sample plots over a number of years may lead to a clearer picture of the general spatial structure of these tussock grasslands, whether these patterns are generally stable over time or how these spatial arrangements are evolving. Re-measuring permanent sample plots over time also has the advantage of reducing between measurement variation and problems with comparing plots from different sites.

This research also leads to further questions, particularly focusing on quantifying the effects of structural fragmentation by *H. pilosella* on other organisms in short tussock grasslands. Of particular interest is the effect on invertebrates and native lizards, as these form the main constituents of many trophic levels in this ecosystem, and primary pollinators for many native herbs. In addition, changes in the quality, quantity and behaviour of pollinators; as well as the changes in microsite characteristics through habitat breakdown, will also affect the regeneration of many plant species. Regeneration failure by these species may allow the escalation of invasion of *H. pilosella.*

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Appendix 1: Formulae

Equation 1: Ripley's *K*-function

$$K(t) = \frac{1}{\hat{\lambda}} \frac{1}{N} \sum_{j=1}^{N} \sum_{j \neq i} k_{ij}$$

where:

t is the scale or distance being examined

$$\hat{\lambda} = \frac{N}{S}$$

N is the number of points

S is size of area

K_{ij} equals 1 if the distance between points i and j is less than t

K_{ij} equals 0 if the distance between point i and j is greater than t

Equation 2: Ripley's K_{12}-function

$$K_{12}(t) = \frac{1}{\hat{\lambda}} \frac{1}{N} \sum_{j=1}^{N} \sum_{j \neq i} k_{ij}$$

where:

t is the scale or distance being examined

$$\hat{\lambda} = \frac{N}{S}$$

N is the number of points

S is size of area

K_{ij} equals 1, if the distance between points i of species 1, and j of species 2 is less than t

K_{ij} equals 0, if the distance between point i of species 1, and j of species 2 j is greater than t

Equation 3: Calculating significance level of a Monte Carlo envelope

$$\alpha = \frac{2(nrank)}{(1 + nsim)}$$

where:

α is the significance level

nrank is the mth lowest and mth highest values i.e. where using the maximum and minimum values, *nrank* = 1

nsim is the number of simulations

As 100 simulations, and the maximum and minimum values were used for all Monte Carlo analyses in this thesis, $\alpha = 0.0198$.

Equation 4: Join Count Statistics

Expected values and variances of joins of the same type:

$$E(x) = \frac{wn_r^{(2)}}{2n^{(2)}}$$

$$Var = \frac{1}{4}\left[\frac{2S_1 n_r^{(2)}}{n^{(2)}} + \frac{(S_2 - 2S_1)n_r^{(3)}}{n^{(3)}} + \frac{(W^2 + S_1 - S_2)n_r^{(4)}}{n^{(4)}} - W^2\left(\frac{n_r^{(2)}}{n^{(2)}}\right)^2\right]$$

Expected values and variances of joins of different types:

$$E(x) = \frac{Wn_r n_s}{n^{(2)}}$$

$$Var = 1/4\left[\frac{2S_1 n_r n_s}{n^{(2)}} + \frac{(S_2 - 2S_1)n_r n_s (n_r + n_s - 2)}{n^{(3)}} + \frac{4(W^2 + S_1 - S_2)n_r^{(2)} n_s^{(2)}}{n^{(4)}} - 4W^2\left(\frac{n_r n_s}{n^{(2)}}\right)^2\right]$$

$$Z - value = \frac{(Obs - E(x))}{SD}$$

where:

E(x) is the expected join count if the pattern of joins is completely spatially random

Var is the estimated variation of join counts

W is the sum of the matrix of weights (W_{ij}) given to joins except diagonals

n is the number of cells

nr is the number of cells of colour r

ns is the number of cells of colour s

$n^{(2)} = n(n-1)$

$n^{(3)} = n(n-1)(n-2)$, and so forth.

Obs = observed join counts

$$S_1 = \frac{1}{2}\sum_{ij}\left(W_{ij} + W_{ji}\right)^2$$

$S_2 = \sum_{i=1}^{n}\left(W_{i\cdot} + W_{\cdot j}\right)^2$, where Wi· and W·i are the sums of the ith row and ith column

Appendix 2: Common and Scientific Species Names

Common Name	Species Name
Bidibid	*Acaena inermis*
Brown-top	* *Agrostis capillaris*
Kopoti	*Anisotome aromatica*
	Anisotome flexuosa
Sweet vernal	* *Anthoxanthum odoratum*
	Brachyglottis bellidioides
Native broom	*Carmichaelia vexillata*
Dainty daisy	*Celmisia gracilenta*
Purging flax	* *Cerastium fontanum*
Red tussock	*Chionochloa rubra*
Wineberry coprosma	*Coprosma atropurpurea*
Creeping coprosma	*Coprosma perpusilla*
Grey woollyhead	*Craspedia lanata*
	Discaria toumatou
Hard tussock	*Festuca novae-zelandiae*
Cranesbill	*Geranium sessiliflorum*
	Hebe buchananii
Slender everlasting	*Helichrysum filicaule*
	Hieracium caespitosum
Mouse-ear hawkweed	* *Hieracium pilosella*
King devil hawkweed	* *Hieracium praealtum*
	Hypochoeris radicata
Yorkshire fog	* *Holcus lantus*
Patotara	*Leucopogon fraseri*
	Leptinella spp.
Purging flax	* *Linum catharticum*
Red wood rush	*Luzula rufa*
Small grassland orchid	*Microtis oligantha*
Black beard lichen	*Neuropogon ciliatus*
Adder's tongue	*Ophioglossum coriaceum*
	Ourisia spp.
Native daphne	*Pimelea oreophila*
Blue tussock	*Poa colensoi*
	Poa maniototo
	Poa novae-zelandiae
Wire moss	*Polytrichum juniperinum*
Onion-leaved orchid	*Prasophyllum colensoi*
	Pyrrhanthera exigua
Woolly moss	*Racomitrium lanuginosum*
Mat daisy	*Raoulia australis*
Mat daisy	*Raoulia hookeri*
Mat daisy	*Raoulia parkii*
Mat daisy	*Raoulia subsericea*
Dwarf buttercup	*Ranunculus cheesemanii*
Sheep's sorrell	* *Rumex acetosella*
	Scleranthus uniflorus
Haresfoot trefoil	* *Trifolium arvense*
White clover	* *Trifolium repens*

Field speedwell	* *Veronica arvensis*
	Viola cunninghamii
Harebell	*Wahlenbergia albomarginata*

* Naturalised species

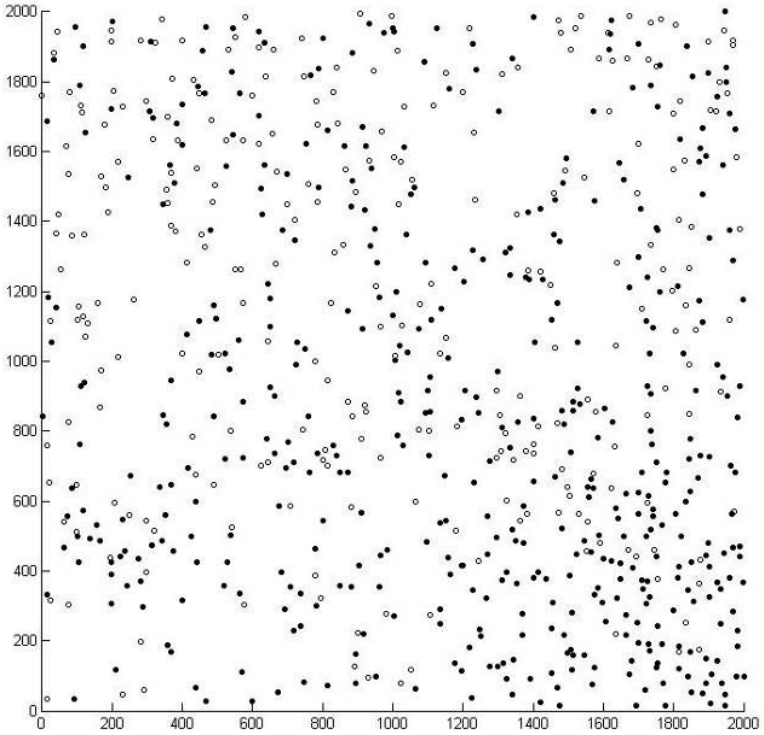
Appendix 3: Tussock plot maps

Legend

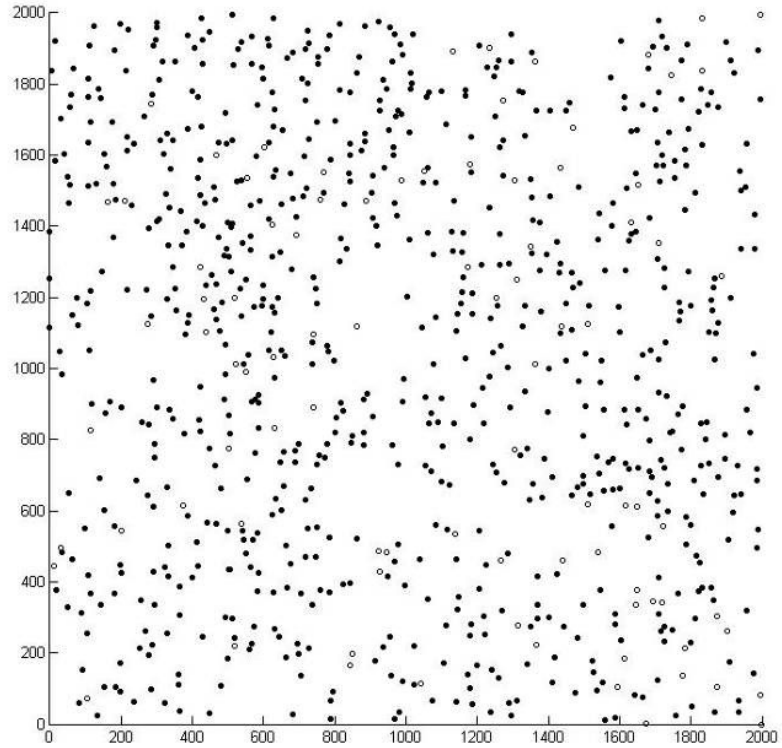
Tussock symbol	Species
filled circle	*Festuca novae-zelandiae*
empty circle	*Poa colensoi*
empty square	*Poa novae-zelandiae*

All maps are proportionally scaled, and both *X* and *Y* axes are in cm.

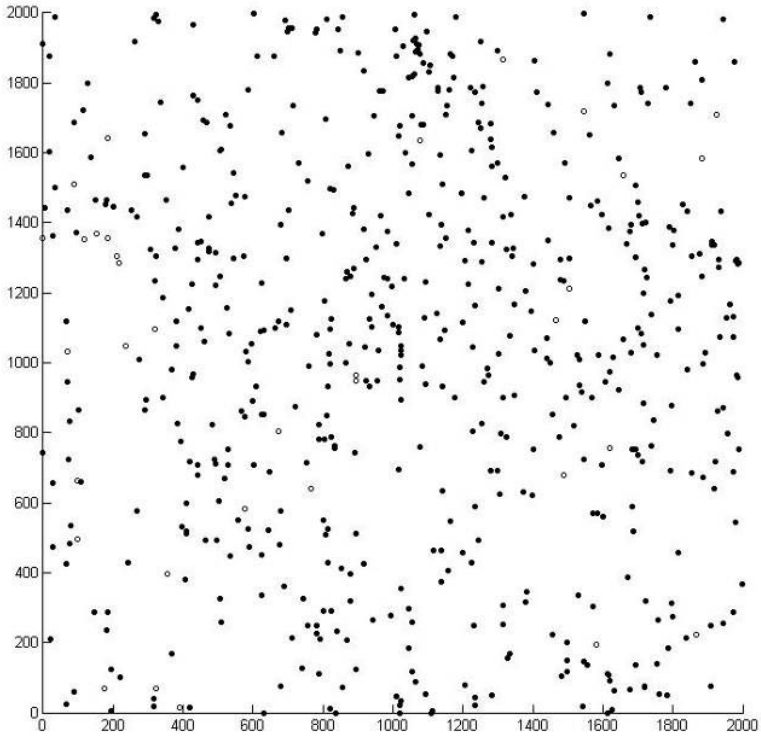
Tussock Plot 1



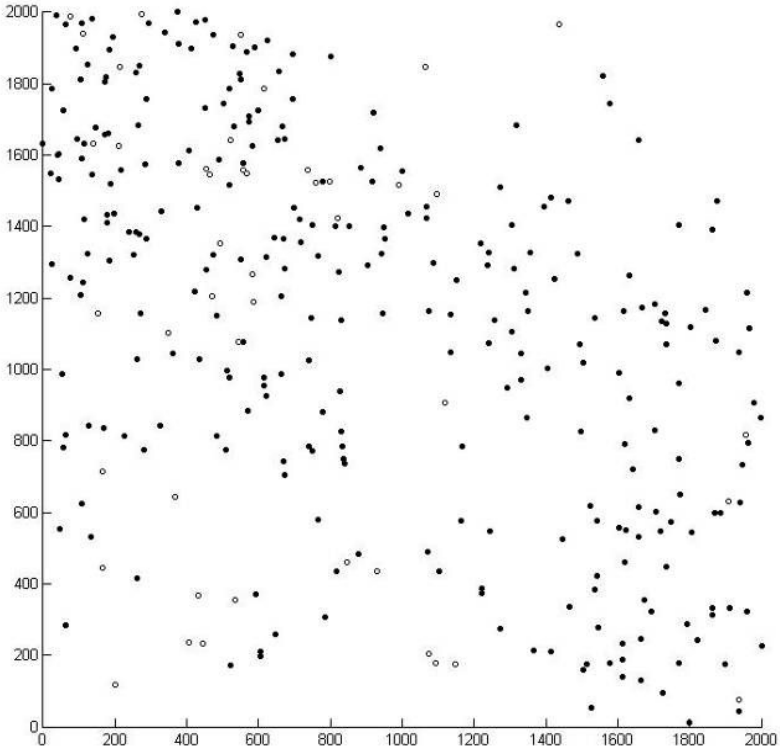
Tussock Plot 2



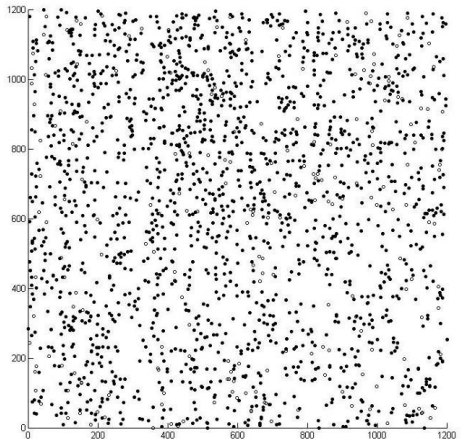
Tussock Plot 3



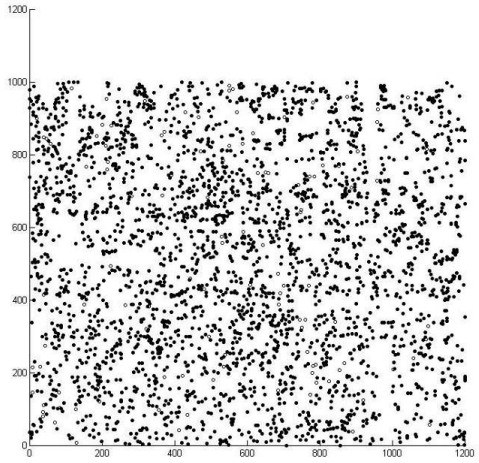
Tussock Plot 4



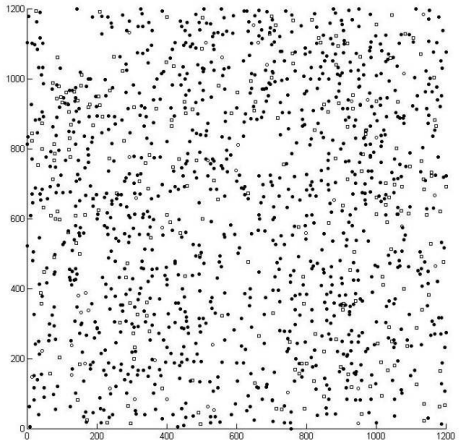
Tussock Plot 5



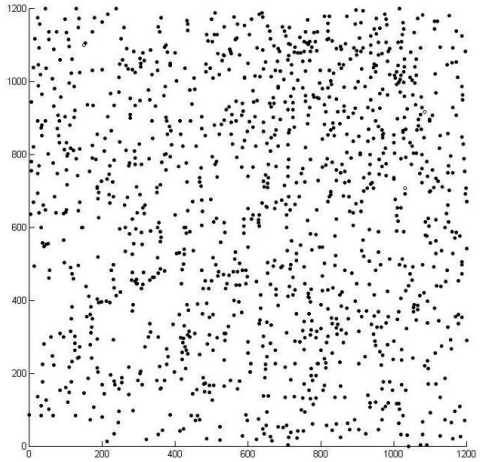
Tussock Plot 6



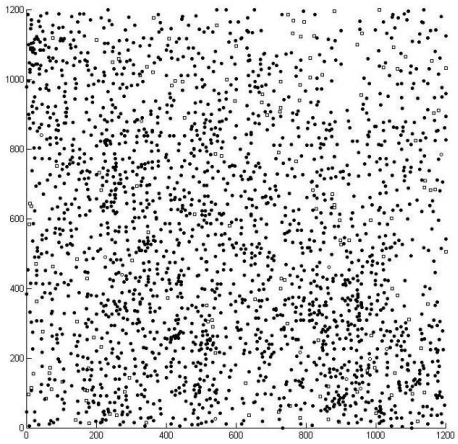
Tussock Plot 7



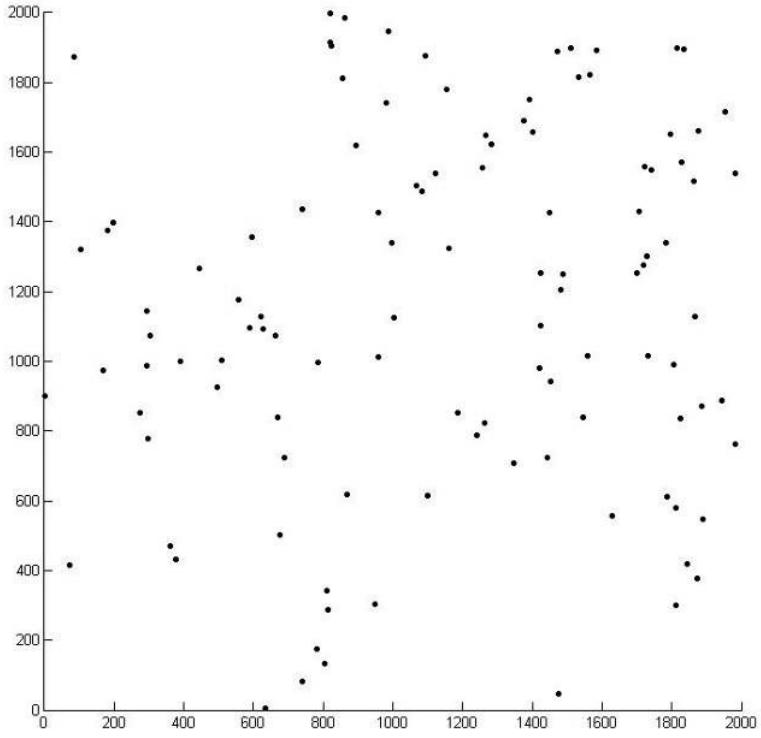
Tussock Plot 8



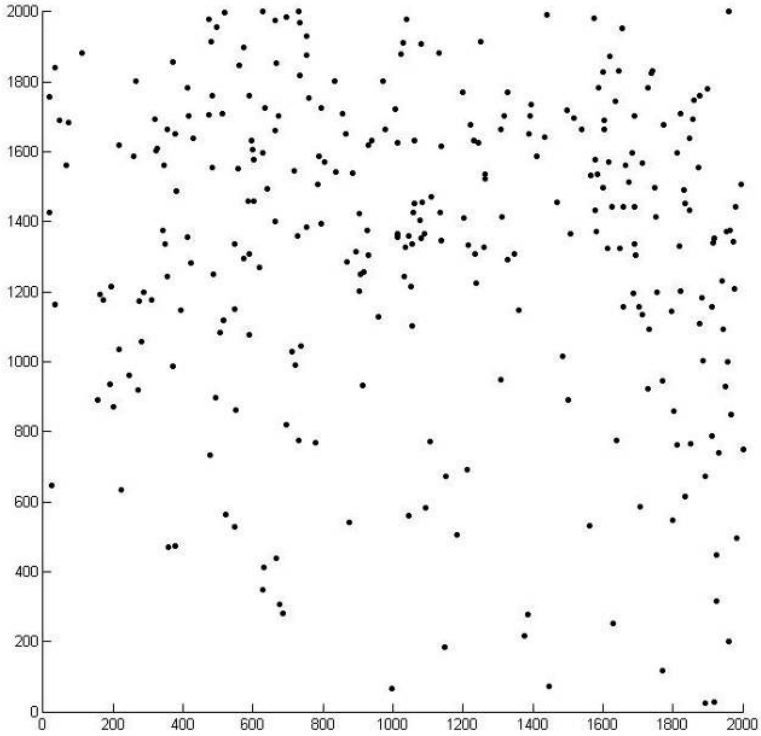
Tussock Plot 9



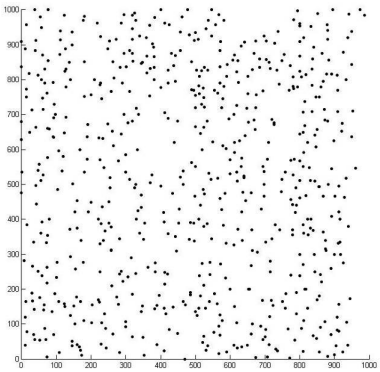
Tussock Plot 10



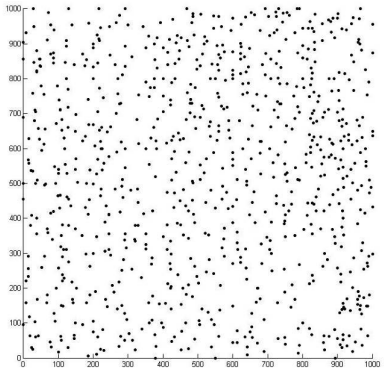
Tussock Plot 11



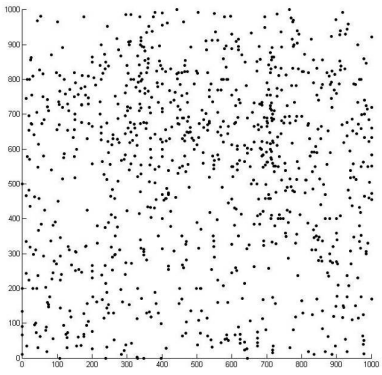
Tussock Plot 12



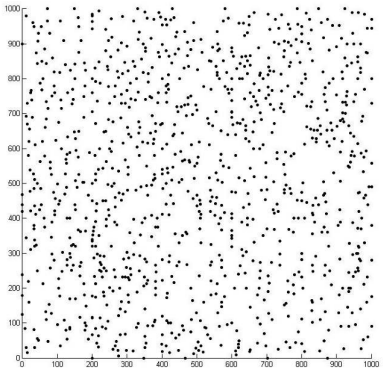
Tussock Plot 13



Tussock Plot 14



Tussock Plot 15



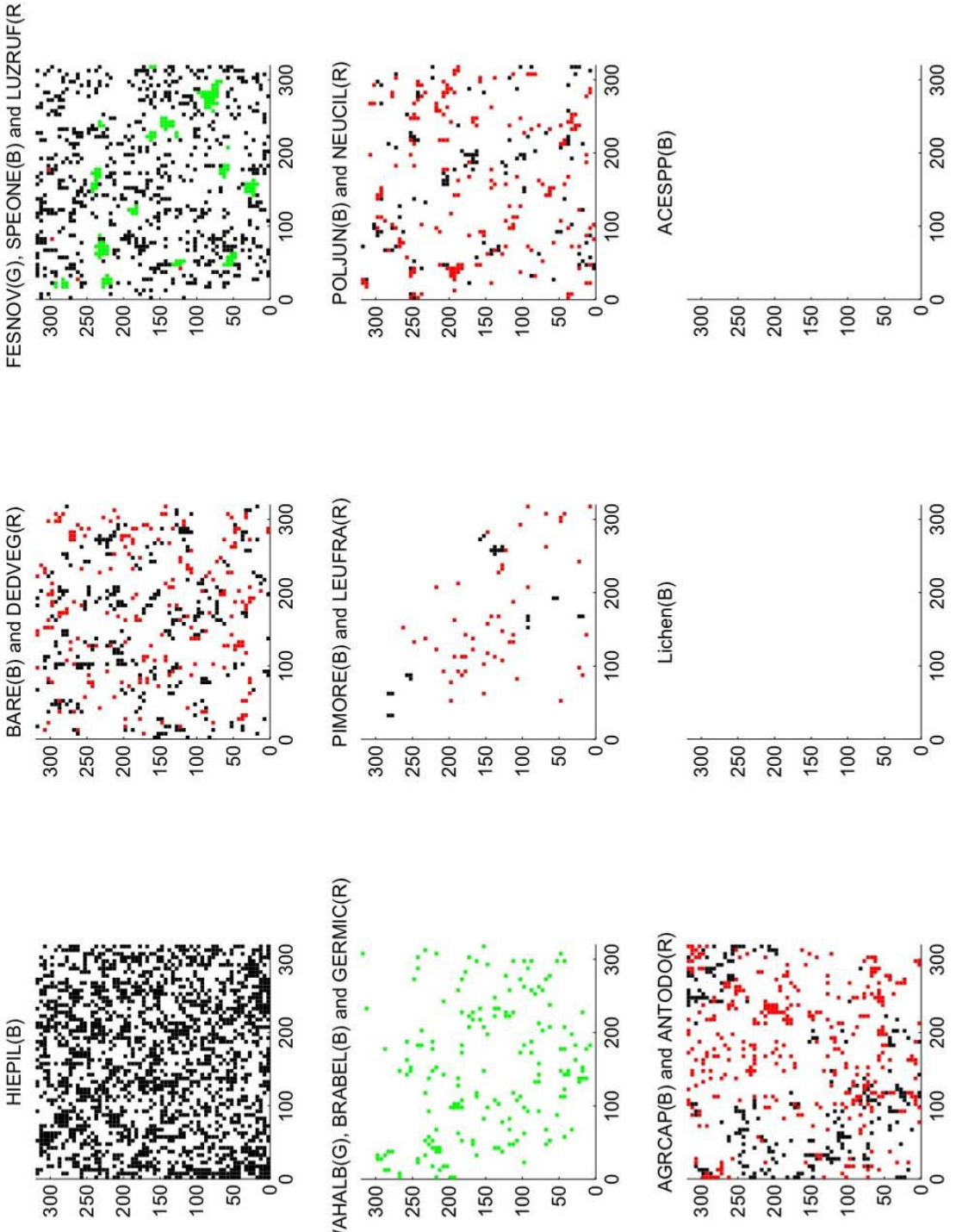
Appendix 4: Full diversity plot maps

Legend

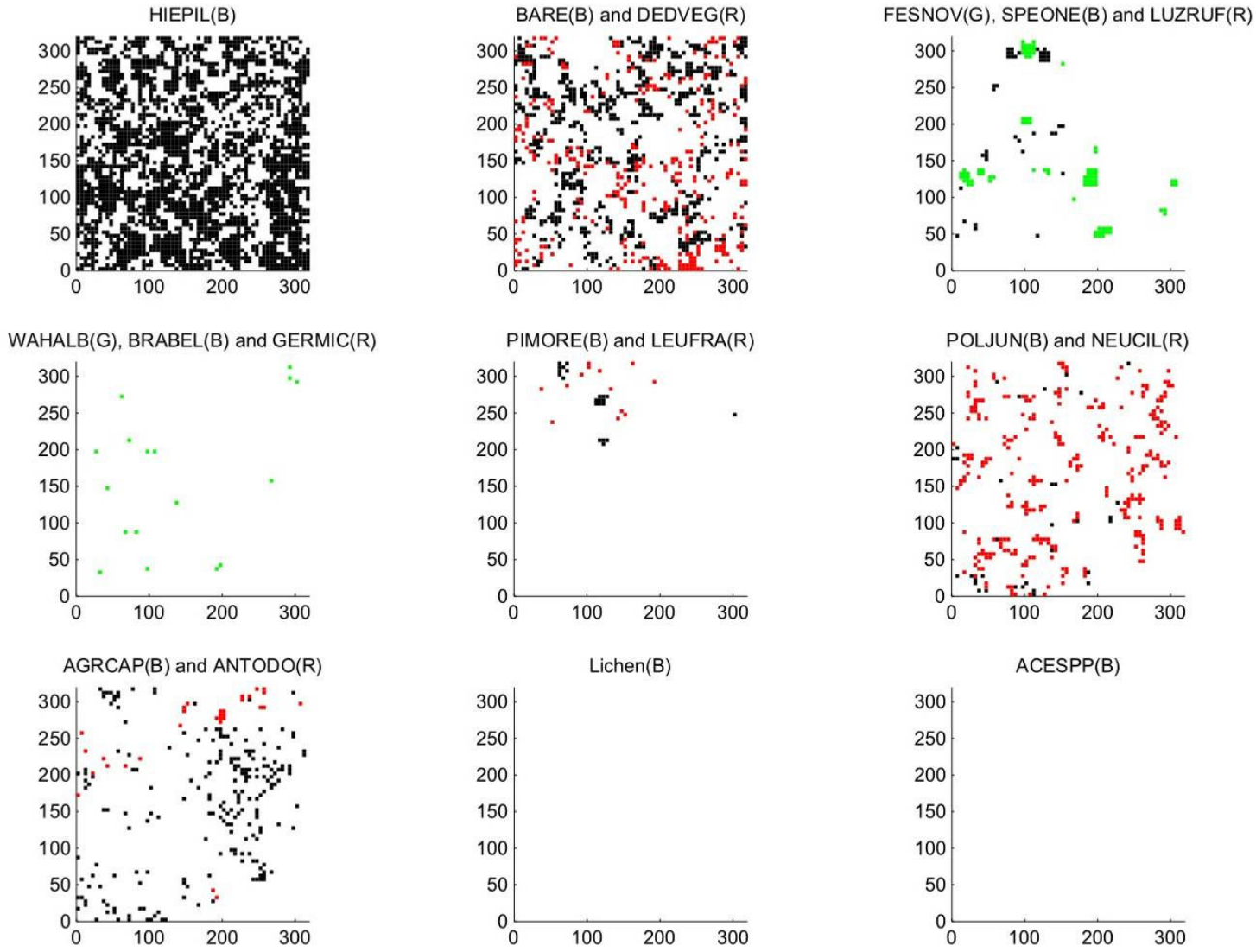
Full Diversity Code	Species
HIEPIL	*Hieracium pilosella*
BARE	Bare ground
DEDVEG	Dead vegetation
FESNOV	*Festuca novae-zelandiae*
SPEONE	*Pyrranthera exigua and Poa maniototo*
LUZRUF	*Luzula rufa*
WAHALB	*Wahlenbergia albomarginata*
BRABEL	*Brachyglottis bellidioides*
GERMIC	*Geranium sessiliflorum*
PIMORE	*Pimelea oreophilla*
LEUFRA	*Leucopogon fraseri*
POLJUN	*Polytrichum juniperum*

Code	Colour
(R)	Red
(B)	Black
(G)	Green

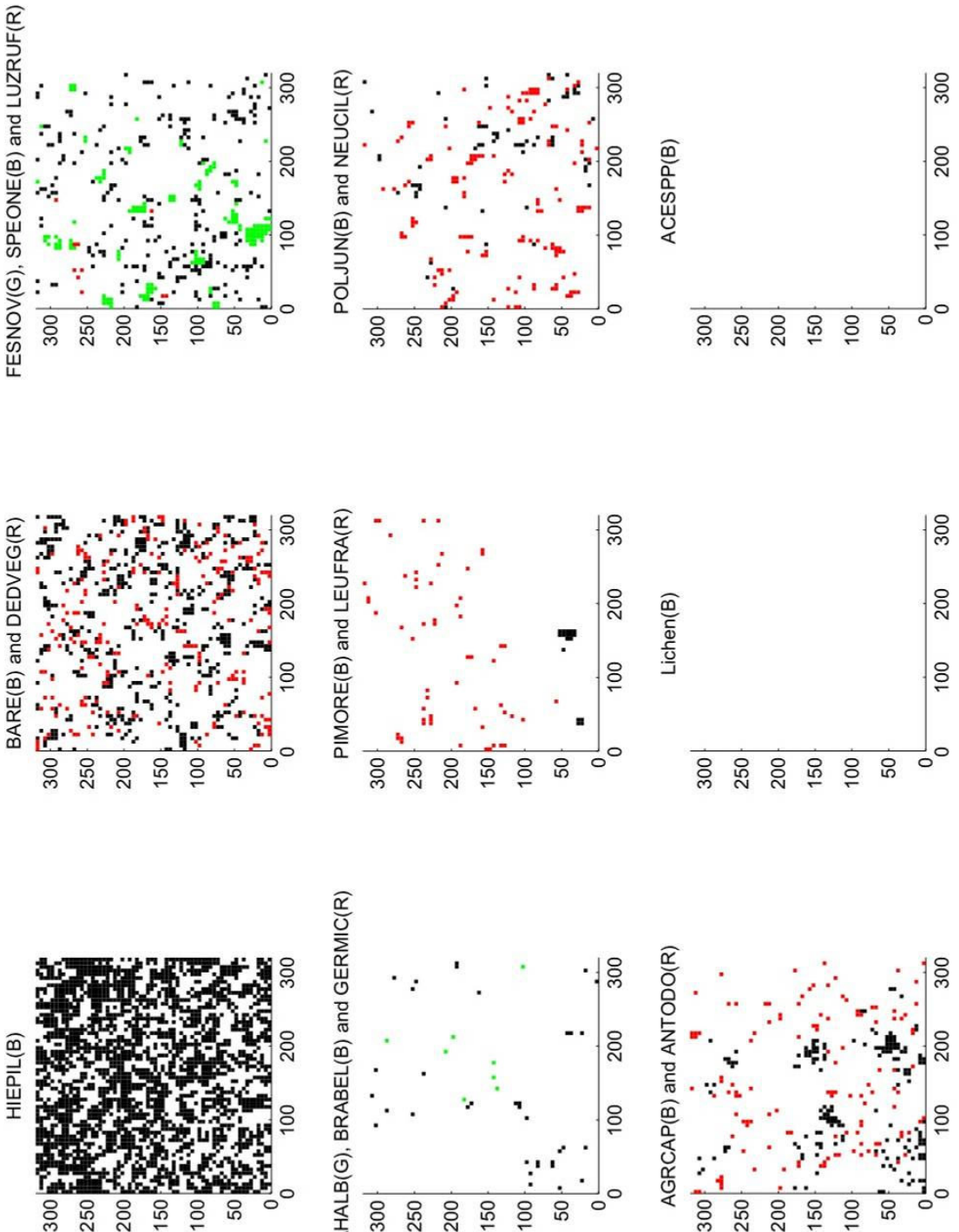
Full Diversity Plot 1



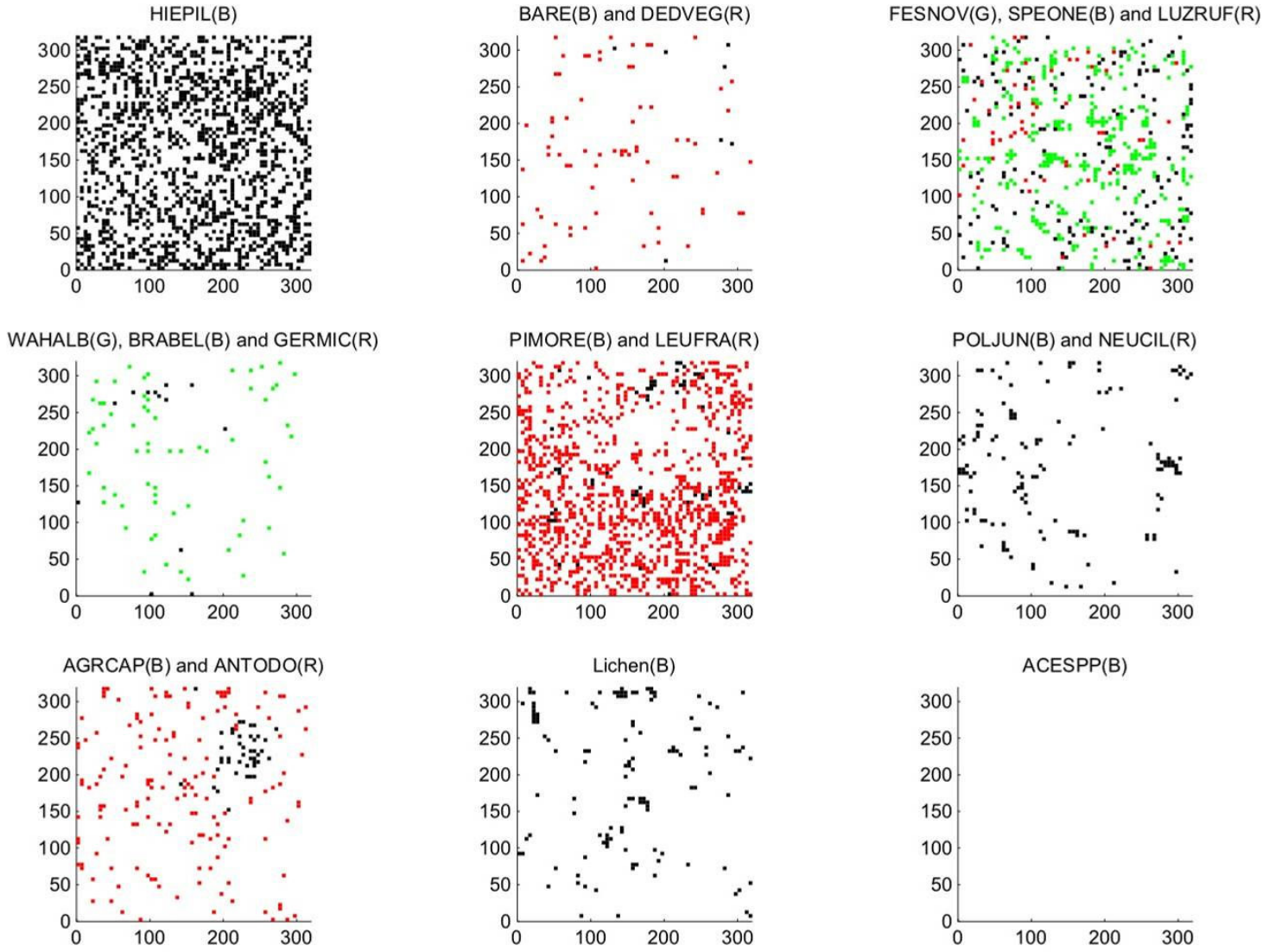
Full Diversity Plot 2



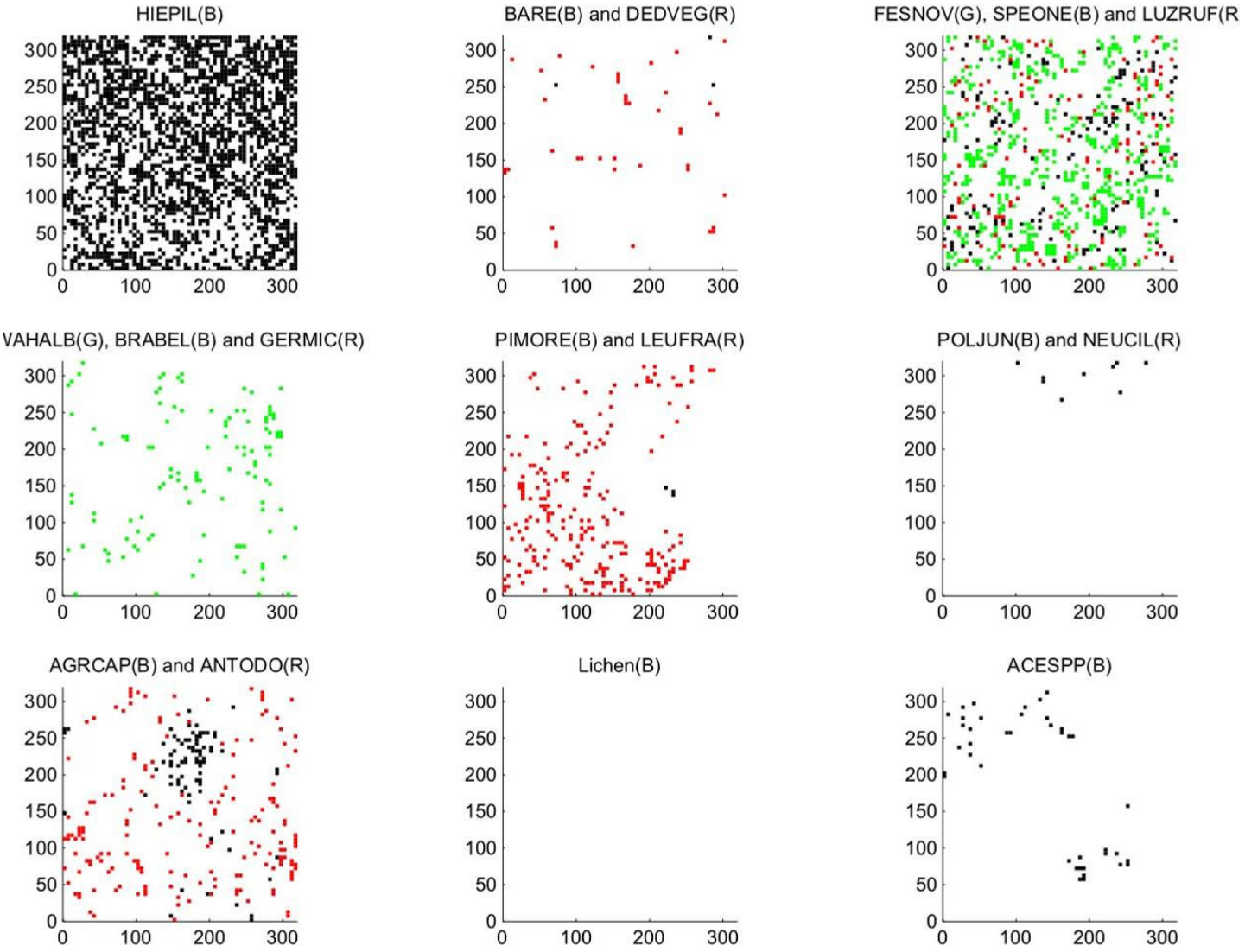
Full Diversity Plot 3



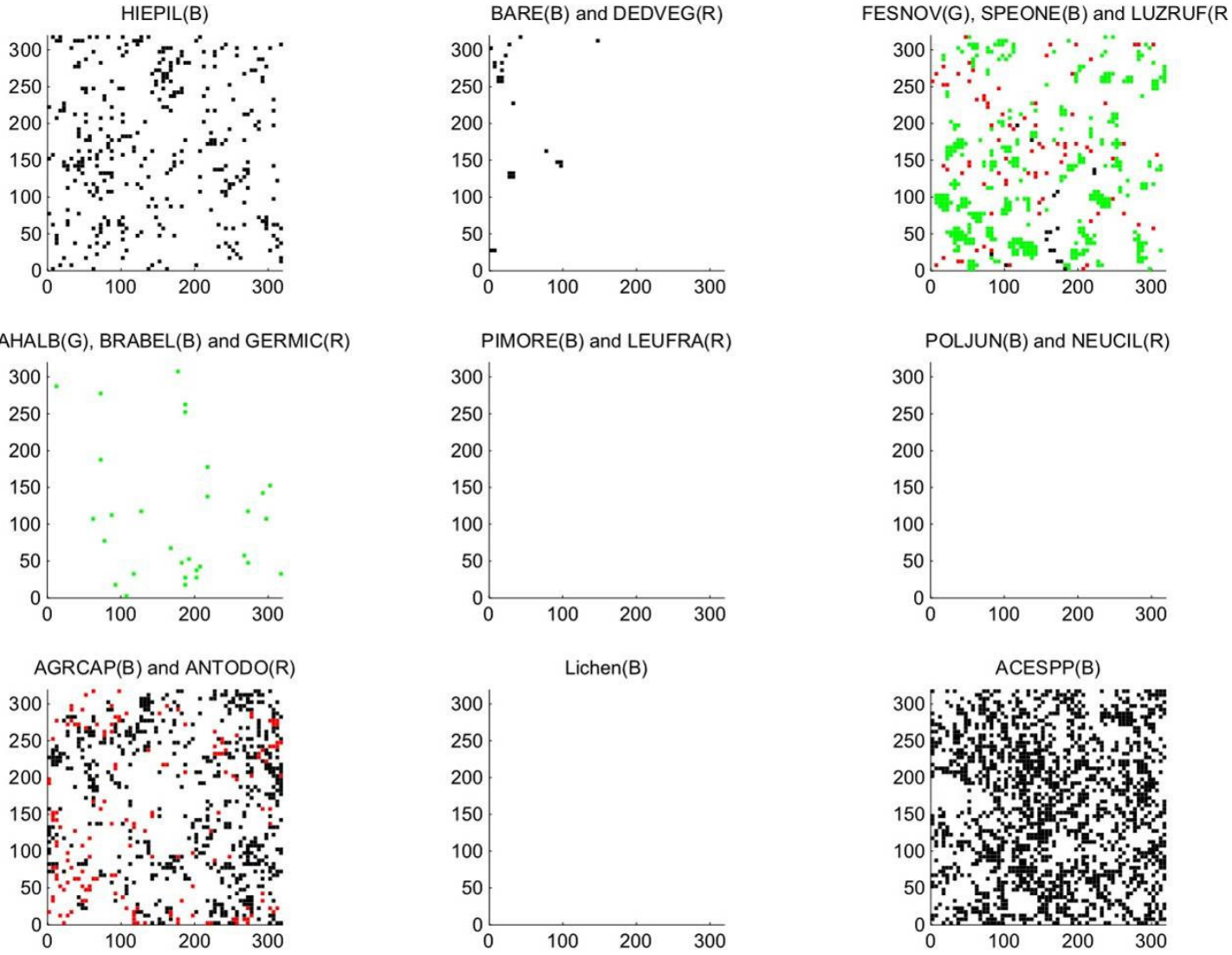
Full Diversity Plot 4



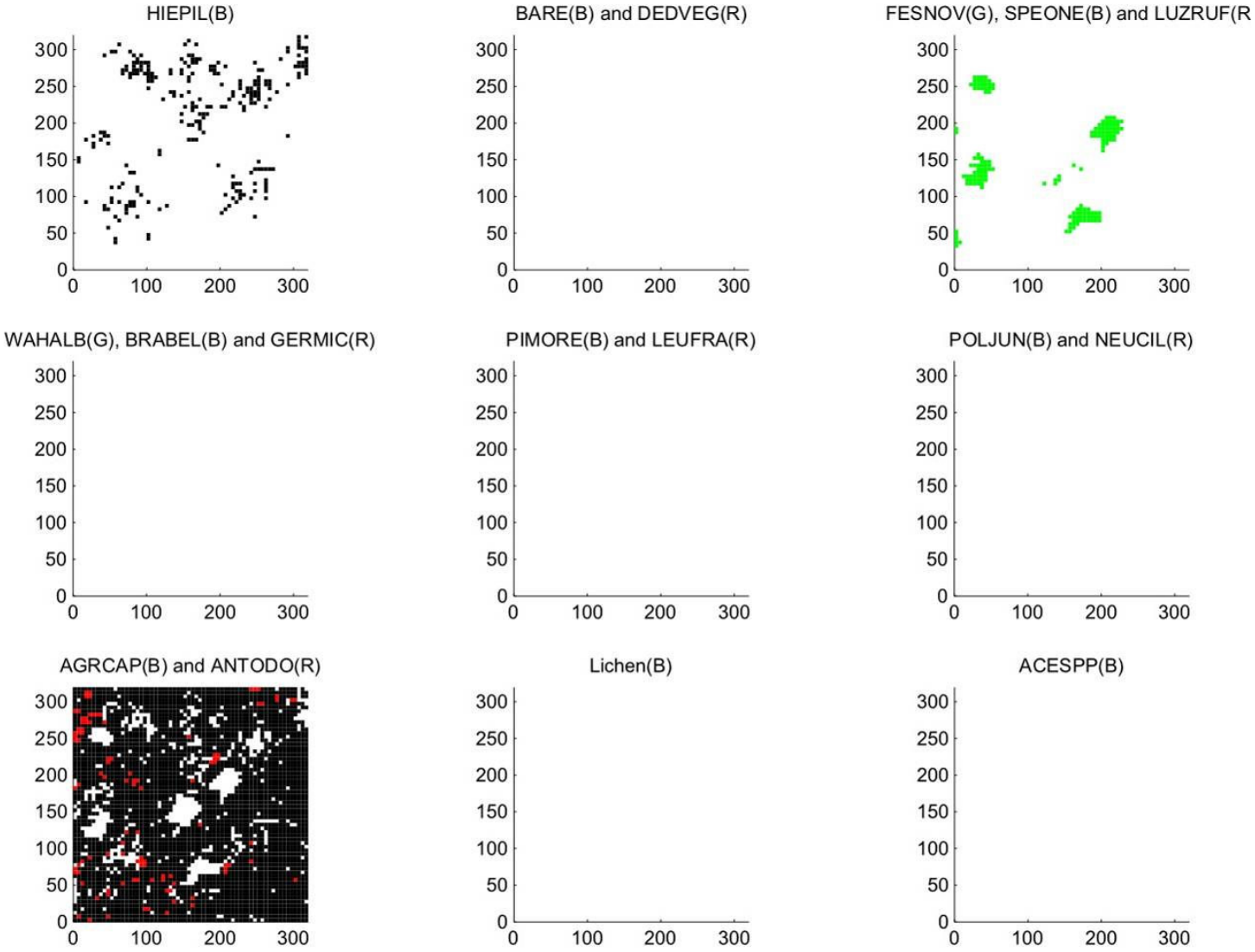
Full Diversity Plot 5



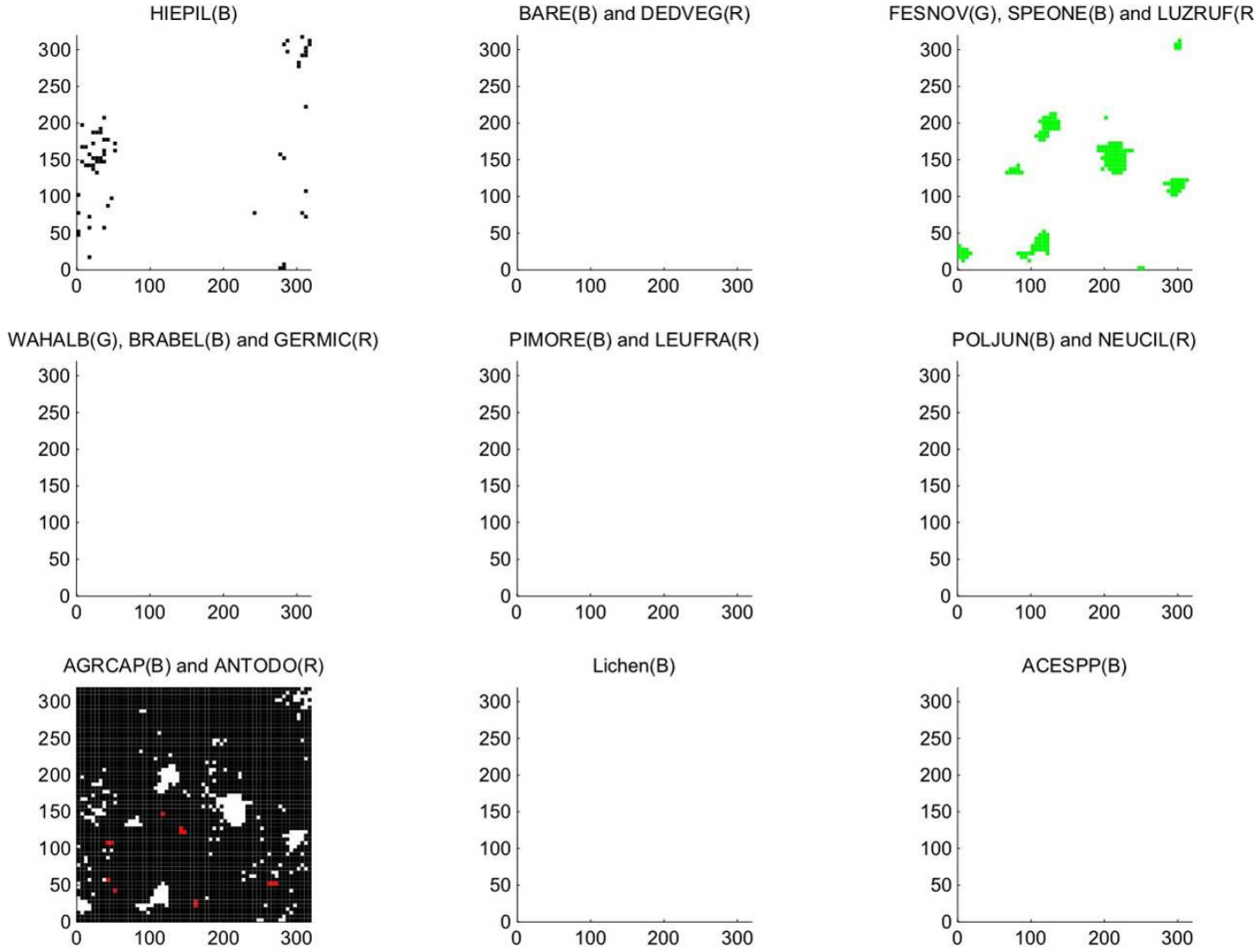
Full Diversity Plot 6



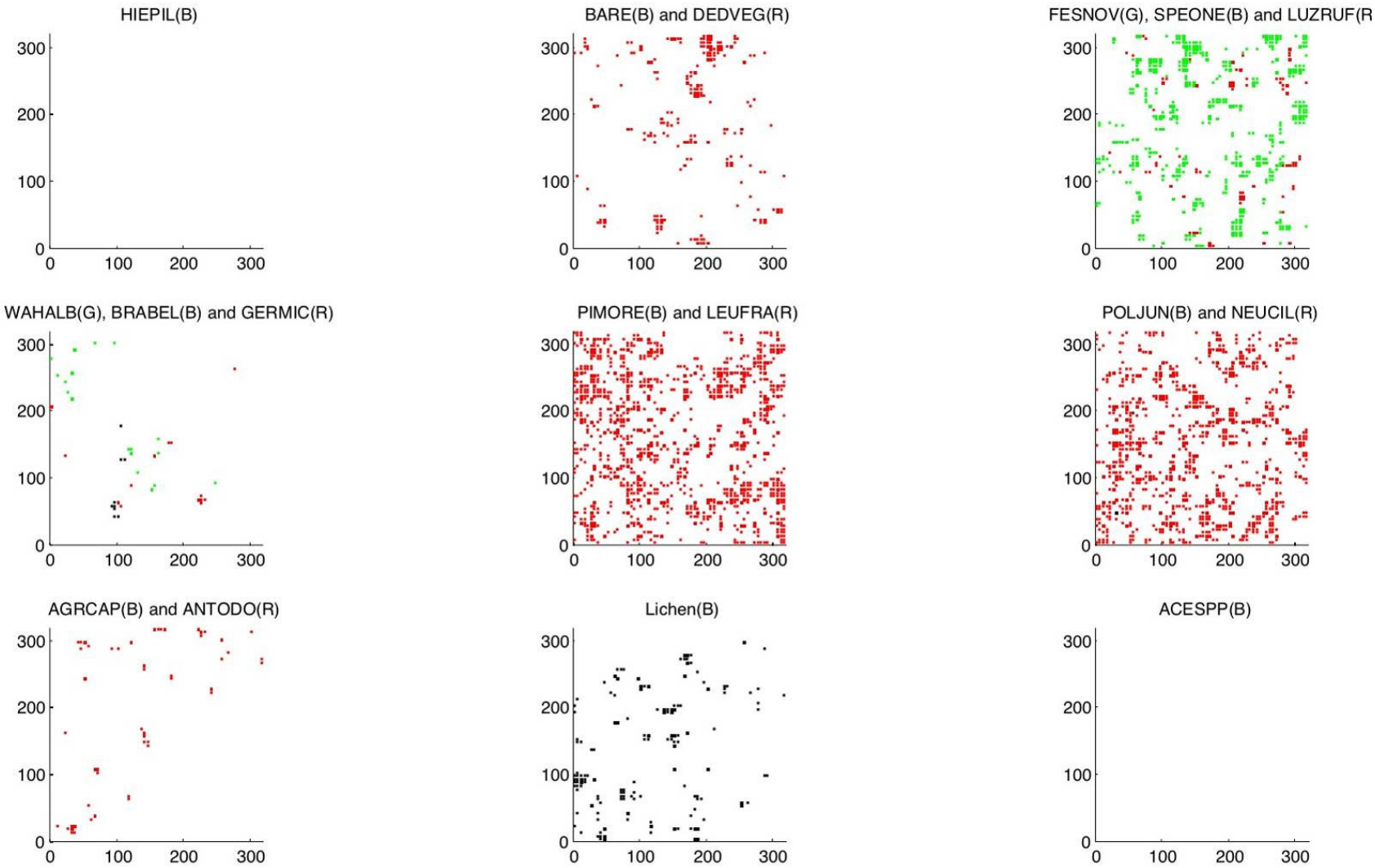
Full Diversity Plot 7



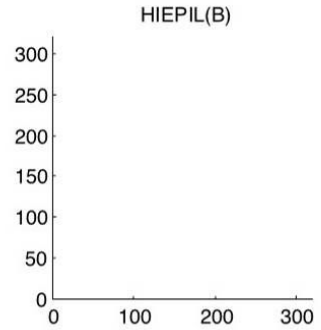
Full Diversity Plot 8

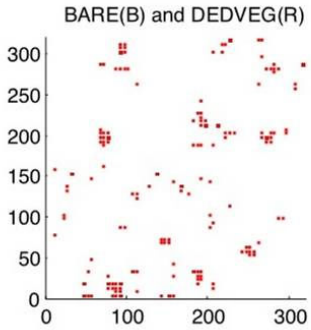


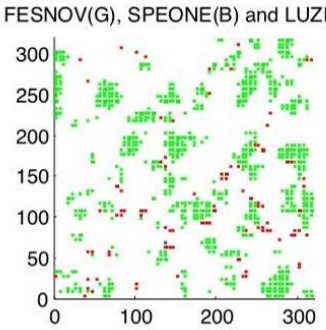
Full Diversity Plot 9

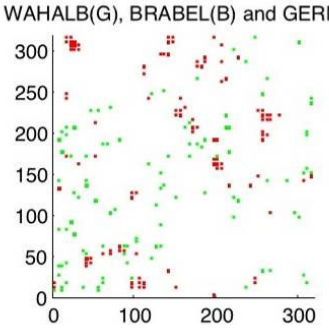


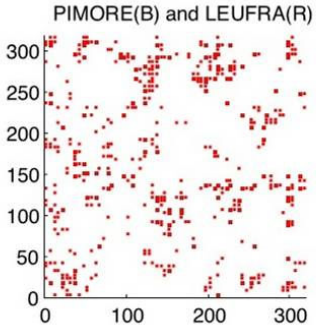
Full Diversity Plot 10

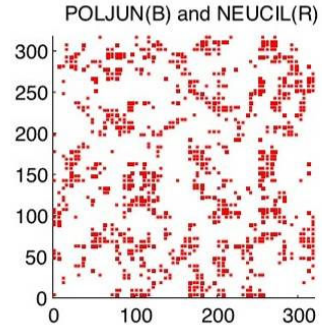


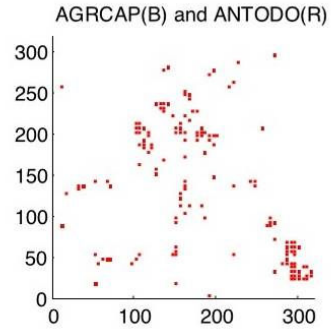


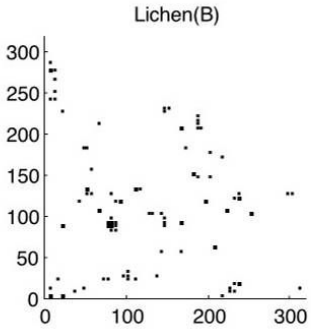


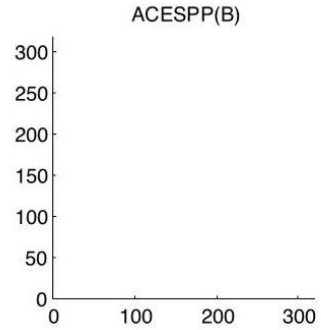












Full Diversity Plot 11